FERNANDO MASSAYUKI ASSEGA

REVISÃO TAXONÔMICA E FILOGENIA DO GÊNERO *ANOSTOMOIDES* PELLEGRIN, 1909 (CHARACIFORMES) COM BASE EM CARACTERES MORFOLÓGICOS E MORFOLÓGICOS E DESCRIÇÃO DE UM NOVO GÊNERO DE ANOSTOMIDAE

Londrina
2018

Revisão taxonômica e filogenia do gênero *Anostomoides* Pellegrin, 1909 (Characiformes) com base em caracteres morfológicos e moleculares e descrição de um novo gênero de Anostomidae

Centro de Ciências Biológicas –
CCB Programa de Pós-Graduação em Ciências
Biológicas Orientador: José Luís Olivan
Birindelli
Orientado: Fernando Massayuki Assega

Londrina – Paraná
2018

FERNANDO MASSAYUKI ASSEGA

REVISÃO TAXONÔMICA E FILOGENIA DO GÊNERO *ANOSTOMOIDES* PELLEGRIN, 1909 (CHARACIFORMES) COM BASE EM CARACTERES MORFOLÓGICOS E MORFOLÓGICOS E DESCRIÇÃO DE UM NOVO GÊNERO DE ANOSTOMIDAE

Tese apresentada ao Programa de Pós-graduação em Ciências Biológicas da Universidade Estadual de Londrina, como requisito parcial à obtenção do título de Doutor em Ciências Biológicas (Biodiversidade e Conservação de Habitats Fragmentados).

Orientador: Prof. Dr. José Luís Olivan Birindelli

Londrina
2018

Ficha de identificação da obra elaborada pelo autor, através do Programa de Geração Automática do Sistema de Bibliotecas da UEL

A844r Assega, Fernando Massayuki.

Revisão taxonômica e filogenia do gênero *Anostomoides* Pellegrin, 1909 (Characiformes) com base em caracteres morfológicos e moleculares e descrição de um novo gênero de Anostomidae / Fernando Massayuki Assega. - Londrina, 2018.
101 f. : il.

Orientador: José Luís Olivan Birindelli.
Tese (Doutorado em Ciências Biológicas) - Universidade Estadual de Londrina, Centro de Ciências Biológicas, Programa de Pós-Graduação em Ciências Biológicas, 2018.
Inclui bibliografia.

1. Sistemática - Tese. 2. Piau - Tese. 3. América do Sul - Tese. 4. Região Neotropical - Tese. I. Birindelli, José Luís Olivan. II. Universidade Estadual de Londrina. Centro de Ciências Biológicas. Programa de Pós-Graduação em Ciências Biológicas. III. Título.

CDU 574

FERNANDO MASSAYUKI ASSEGA

REVISÃO TAXONÔMICA E FILOGENIA DO GÊNERO *ANOSTOMOIDES* PELLEGRIN, 1909 (CHARACIFORMES) COM BASE EM CARACTERES MORFOLÓGICOS E DESCRIÇÃO DE UM NOVO GÊNERO DE ANOSTOMIDAE

Tese apresentada ao Programa de Pós-graduação em Ciências Biológicas da Universidade Estadual de Londrina, como requisito parcial à obtenção do título de Doutor em Ciências Biológicas (Biodiversidade e Conservação de Habitats Fragmentados).

BANCA EXAMINADORA

_____

Orientador: Prof. Dr. José Luís Olivan Birindelli
Universidade Estadual de Londrina – UEL

_____

Prof. Dr. Cristiano Luis Rangel Moreira
Universidade Federal do Rio de Janeiro – UFRJ

_____

Prof. Dr. Gabriel de Souza da Costa e Silva
Universidade Estadual de Londrina – UEL

_____

Prof. Dr. Júlio Cesar Garavello
Universidade Federal de São Carlos – UFSCar

_____

Prof. Dr. Oscar Akio Shibatta
Universidade Estadual de Londrina – UEL

Londrina, 19 de dezembro de 2018.

“Quanto mais aumenta nosso conhecimento,
mais evidente fica nossa ignorância”.
(John F. Kennedy)

“Tenho a impressão de ter sido uma criança brincando à beira-mar,
divertindo-me em descobrir uma pedrinha mais lisa ou uma concha mais
bonita que as outras, enquanto o imenso oceano da verdade continua
misterioso diante de meus olhos”.

(Isaac Newton)

“A pior maneira de não chegar a
determinado lugar é pensar que já está lá”.

Desconhecido

Dedico:

À Ana Paula, minha querida esposa, à minha sogra Solange, e aos meus pais Nelson e Maria, meus grandes incentivadores, que sempre acreditaram em mim, com muito amor, apoio e paciência.

AGRADECIMENTOS

Agradeço especialmente ao meu orientador e amigo, prof. Dr. José Luís Olivan Birindelli pela dedicação à função de orientador, pela confiança dada a mim para desenvolver este trabalho, pela paciência, atenção e compreensão em vários momentos ao longo desta etapa, pelos ensinamentos e a oportunidade de conhecer uma breve parte sobre a sistemática dos anostomídeos, em especial *Anostomoides*.

Ao professor e amigo, Dr. Oscar Akio Shibatta, a quem sou muito grato pelos ensinamentos, pela paciência no decorrer desses anos de convívio diário desde a graduação, passando pelo mestrado e agora o Doutorado, que me permitiram crescer como pessoa e como profissional.

Ao professor e amigo, Dr. Fernando Jerep, pelas sugestões e questionamentos em relação a tese, pela paciência ao me orientar nas mais diversas dúvidas, pelas palavras de incentivo que revigoram o meu ânimo e pelo convívio diário com momentos descontraídos na hora do café.

Aos professores: Dr. Brian Sidlauskas (OSU) e Dr. Jansen Zuanon (INPA) pelas valiosas discussões e sugestões para a conclusão deste trabalho.

Aos professores: Dr. Mark Sabaj (ANSP), Dr. Jonathan Armbruster e David Werneke (AUM), Dra. Lúcia Rapp Py-Daniel (INPA), Dr. Leandro Sousa (LIA), Dr. Marcelo Britto (MNRJ), Dr. Hernan Ortega (MUSM), Dr. Alessio Datovo, Dr. Heraldo Britski, Dr. Osvaldo Oyakawa e Dr. Naércio Menezes (MZUSP), Dra. Carla Pavanelli (NUPÉLIA), Dr. Marcelo Britto (MNRJ), Dr. Walmor Wosiacki (MPEG), Dra. Mariluce Rezende Messias e a bióloga Ângela Soares (UFRO-IC) pelo empréstimo do material utilizado para a confecção dessa tese.

Aos professores: Dr. Claudio Oliveira e Dr. Bruno Melo (LBP), Dr. Alessio Datovo, Dr. Heraldo Britski, Dr. Osvaldo Oyakawa e Dr. Naércio Menezes (MZUSP) e à Dra. Lúcia Rapp Py-Daniel (INPA) pela recepção amistosa nas coleções ictiológicas em que atuam.

Agradeço aos professores: Dr. Alessio Datovo (MZUSP), Dra. Camila Ribas (INPA), Dr. Mark. Sabaj (ANSP – Projeto iXingu), Dr. Tomas Hrbek e Dra. Izeni Farias (UFAM – Projeto CNPq/SISBIOTA – BioPHAM) pelo empréstimo dos tecidos e vouchers.

Agradeço os estagiários e técnicos de laboratório que acondicionaram com muito zelo o material enviado como empréstimo.

Sou grato também ao Daniel Le e Kevin Swagel do Field Museum of Natural History, Chicago (FMNH) que disponibilizaram as fotos do holótipo de *Schizodontopsis laticeps* (FMNH 53359) que ilustraram essa tese.

À Universidade Estadual de Londrina e ao Programa de Pós-Graduação em Ciências Biológicas da Universidade Estadual de Londrina.

O presente trabalho foi realizado com apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Código de Financiamento 001.

Aos amigos Vitor Abraão, Nathália Rizzo Friol e Willian Ohara por terem me recebido com muito carinho e hospedado durante a minha visita ao MZUSP.

A tia Zenaide, pessoa de pequeno tamanho, mas de coração enorme que não cabe no peito. por ter me hospedado durante as minhas visitas à São Paulo;

A tia Lourdes e a Solange Maria pela excelente e animada companhia, sempre dispostas e alegre;

Ao amigo Michel Gianeti, por ter me recebido tão bem durante as minhas visitas ao MZUSP, pela disposição de sempre ajudar com tanta atenção e carinho.

Aos amigos de Manaus: Alessandro Bifi, Douglas Bastos, Isabel Soares, Rafaela Ota e Shizuka Hashimoto pela recepção amistosa. Um obrigado especial à Rafaela Ota por ter me recebido com muito carinho durante a minha visita à Manaus, ao Alessandro Bifi, por ter me hospedado tão gentilmente.

Ao Bruno Melo e à Beatriz Dorini por terem me recebido com muita atenção e paciência e ao grande amigo Gabriel de Souza Costa e Silva, pela recepção e hospedagem durante as minhas visitas ao Laboratório de Biologia e Genética de Peixes de Botucatu (LBP).

Aos companheiros de laboratório do Museu de Zoologia da Universidade Estadual de Londrina (MZUEL) em especial à amiga Fernanda (Nervosa) Martins, sempre disposta a me ajudar com as dúvidas referentes à taxonomia e filogenia, e a positivismo de que tudo vá se ajeitar; ao Alex Claro pela amizade, companheirismo e otimismo de que tudo dará certo; ao Raul pela amizade sempre presente durante todo o Doutorado, além da ajuda na confecção dos mapas e nas diversas sugestões sobre a tese. Aos técnicos de laboratório, em especial ao Edson Santana pela amizade, companheirismo, as conversas no dia-a-dia e pela sua disposição de sempre estar pronto para ajudar.

À minha grande amiga/ irmã Kátia Real pelo exemplo de determinação, otimismo, disposição e companheirismo, mesmo que às vezes “dias nublados” tenham ocorrido;

Agradeço à minha querida sogra Solange pelo apoio em todos os momentos, além dos lanchinhos da tarde, das feijoadas e bacalhoadas deliciosas preparadas com muito amor e carinho.

À família Pelegrinelli, em especial as tias Lourdes, Maria Helena e Zenaide sempre atenciosas e preocupadas comigo e com a Ana Paula, sempre com uma palavra de incentivo e apoio.

Agradeço muito, especialmente, à Ana Paula, minha querida esposa, minha companheira, minha fonte de inspiração, parceira de vida, amiga e confidente que sempre esteve e continua ao meu lado ao longo destes anos, sempre com muito amor, respeito, paciência, compreensão e apoio incondicional para conclusão desta etapa da minha vida.

Por fim, aos meus pais, Nelson e Maria, que são e sempre serão meus pilares, pelo exemplo de vida, amor, por toda compreensão e esforços para que eu pudesse atingir os meus objetivos. Nada disso seria possível sem a educação, dedicação, amor e apoio que sempre me proporcionaram.

ASSEGA, F. M. **Revisão taxonômica e filogenia do gênero *Anostomoides* Pellegrin, 1909 (Characiformes: Anostomoidae) com bases em caracteres morfológicos e moleculares e descrição de um novo gênero de Anostomidae.** 2018. 93 f. Tese (Doutorado em Ciências Biológicas) - Universidade Estadual de Londrina, Londrina, 2018.

RESUMO

O conhecimento sobre sistemática é essencial para os estudos das demais áreas da Biologia. Nesse sentido, os maiores grupos de peixes de água doce, os Siluriformes, Characiformes, Cyprinodontiformes e Gymnotiformes tem sido foco de grandes projetos de pesquisa do Brasil e no mundo. A família Anostomidae (Characiformes) é composta por 15 gêneros e 147 espécies conhecidas popularmente como piaus e aracús. O gênero *Anostomoides* (Anostomidae) possui três espécies nominais: *A. atrianalis, A. laticeps e A. passionis*, sendo a primeira descrita para o rio Orinoco (Venezuela), a segunda para o rio Essequibo (Guiana), e a última para o médio rio Xingu. No entanto, Steindachner (1876) descreveu *Leporinus nattereri*, uma espécie pouco documentada até o momento, com corpo alto e boca supraterminal, semelhante a *A. passionais.* As informações disponíveis sobre *Anostomoides* e suas espécies são insuficientes para diagnosticar as espécies e, portanto, para verificar a validade e distribuição geográfica das mesmas. Desse modo, o presente estudo teve como objetivo: realizar uma revisão taxonômica de *Anostomoides*, reavaliando todas as espécies nominais e suas distribuições geográficas; e testar a monofilia do gênero por meio de uma filogenia com base em caracteres morfológicos e moleculares. Para isso, dados merísticos, morfométricos e moleculares de exemplares depositados em coleções científicas foram obtidos e analisados. A revisão taxonômica não encontrou um caracter morfológico exclusivo para definir o gênero *Anostomoides*. No entanto, demonstrou que *A. laticeps* é sinônimo júnior de *A. atrianalis*, enquanto que *A. passionis* é sinônimo júnior de *Leporinus nattereri*, sendo o último nome então transferido para *Anostomoides* formando a nova combinação: *Anostomoides nattereri*. Posteriormente, uma análise filogenética foi realizada. Para isso, uma matriz de caracteres morfológicos foi obtida na literatura, e os caracteres foram codificados para exemplares das duas espécies de *Anostomoides*. A matriz final foi utilizada numa análise de parcimônia. Paralelamente, dados moleculares de cinco genes foram obtidos no GenBank. Adicionalmente, exemplares das duas espécies de *Anostomoides* foram obtidos e os tecidos sequenciados, e as sequências incluídas na matriz de caracteres moleculares. Esses dados foram então usados para uma análise de Máxima Verossimilhança. Ambas as análises demonstraram que *Anostomoides*, conforme anteriormente definido, é um gênero polifilético. Desta forma, um novo gênero, possivelmente grupo irmão de todos os anostomídeos (ou de todos, exceto *Leporellus*) é descrito detalhadamente e comparado aos demais gêneros de Anostomidae. Os principais caracteres que suportam as hipóteses de relacionamento do gênero novo são discutidos.

Palavras chave: Sistemática. Piau. Aracú. América do Sul. Região Neotropical.

ASSEGA, F. M. **Taxonomic assessment of *Anotomoides* Pellegrin, 1909 (Characiformes: Anostomoidae) using molecular and morphological data and description of a new genus of Anostomidae.** 2018. 93 p. Thesis (Doctoral in Biological Sciences) - Universidade Estadual de Londrina, Londrina, 2018.

ABSTRACT

Systematic knowledge is essential for studies in other areas of Biology. In this sense, the largest groups of freshwater fish, Siluriformes, Characiformes, Cyprinodontiformes and Gymnotiformes have been the focus of major research projects in Brazil and worldwide. The family Anostomidae (Characiformes) is composed of 15 genera and 147 species popularly known as piaus and Aracus. The genus *Anostomoides* (Anostomidae) has three nominal species: *A. atrianalis*, *A. laticeps* and
A. passionis, the first is known for the Orinoco river (Venezuela), the second for the Essequibo river (Guyana), and the latter for the middle Xingu river. However, Steindachner (1876) described *Leporinus nattereri*, a species poorly known so far, with a tall body and supraterminal mouth, similar to *A. passionais*. The available information on *Anostomoides* and its species are insufficient to diagnose the species and, therefore, to verify their validity and geographical distribution. The present study had as goal: to perform a taxonomic revision of *Anostomoides*, re- evaluating all nominal species and their geographic distributions; and to test the monophyly of the genus based on morphological and molecular characters. For this, meristic, morphometric and molecular data of specimens deposited in scientific collections were obtained and analyzed. The taxonomic revision did not find an exclusive morphological character to define the genus *Anostomoides*. However, *A. laticeps* is a junior synonym of *A. atrianalis*, while *A. passionis* is a junior synonym of *Leporinus nattereri*, the latter being then transferred to *Anostomoides* forming the new combination: *Anostomoides nattereri*. Posteriorly, a phylogenetic review of was performed. For this, a morphological character matrix was obtained from the literature, and the characters coded for specimens of the two species of *Anostomoides*. The matrix was used in a parsimony analysis. Concomitantly, molecular data of five genes were obtanined from GenBank. Aditionally, tissue samples of specimens of the two species of *Anostomoides* were obtained, sequenced, and their sequences included in the molecular matrix. These data were analysed using Maximum Likelyhood. Both analyses demonstrated that *Anostomoides*, as previously defined, is a poliphyletic genus. Therefore, a new genus, possibly closely sister to all anostomids (or to all, except *Leporellis*), is described in details and compared to all other genera of Anostomidae. The main characters that support the phylogenetic relationships of the new genus are discussed.

Key words: Systematics. Piau. Aracu. South America. Neotropical region.

LISTA DE FIGURAS

Capítulo 2

LISTA DE TABELAS

Capítulo 1

Capítulo 2

SUMÁRIO

- Introdução geral -

Artigo formatado nas normas da Revista Zootaxa e não será submetido à publicação

Introdução geral

A ordem Characiformes constitui um dos mais diversificados grupos de peixes de água doce é composta aproximadamente por 3657 espécies válidas distribuídas em 24 familias (Fricke *et al*., 2019). Na Ordem Characiformes estão incluídas espécies de grande importância ecológica e econômica no Brasil que são utilizadas na pesca comercial, esportiva e na aquicultura, como por exemplo os curimbatás (Prochilodontidae), piaparas e piaus (Anostomidae), traíras (Erythrinidae), lambaris (Characidae), piranhas e pacus (Serrasalmidae) e dourados (Bryconidae), embora, haja um grande número de espécies de peixes de pequeno porte, principalmente da família Characidae que estão entre os peixes de aquário mais populares do mundo devido a sua diversidade de colorido, sendo um atrativo aos aquaristas, com milhões de indivíduos das mais variada espécies (*e.g. Hyphessobrycon, Paracheirodon e Gymnocorymbus*) sendo exportados anualmente das bacias do rio Amazonas e Orinoco como peixes ornamentais, o que tem gerado importantes divisas para o país, embora seus impactos ambientais ainda não foram estimados nas áreas no qual as espécies foram introduzidas (Chao *et al.*, 2001; Van Der Sleen & Alberts, 2018).

Na Ordem Characiformes, a família Anostomidae é a segunda mais diversa, composta por 148 espécies válidas, distribuídas em 15 gêneros (Fricke *et al*., 2019). As espécies de Anostomidae são popularmente conhecidas no Brasil como piaus, piavas ou aracus. As espécies da família são endêmicas da região Neotropical, sendo amplamente distribuídas desde o norte da Colômbia até regiões sub-temperadas da Argentina (Garavello & Britski, 2003). São peixes que podem ser distinguidos dos demais Characiformes por apresentarem uma única série de três ou quatro dentes grandes e incisiformes em cada pré-maxilar e dentário, e pela ausência de dentes no osso maxilar e no palato (Géry, 1977). A família Anostomidae é um grupo monofilético suportado

por diversas características morfológicas, a maioria delas relacionada ao aparelho branquial e suspensório (Vari, 1983; Sidlauskas & Vari, 2008), e também por dados moleculares (Dillman *et al*., 2016; Mirande, 2018).

Winterbottom (1980), numa ampla revisão taxonômica e filogenética, estudou a subfamília Anostominae, grupo que engloba os gêneros *Anostomus* Scopoli 1777, *Gnatholodus* Myers 1927, *Sartor* Myers & Carvalho 1959, *Synaptolaemus* Myers & Fernández-Yépez 1950, *Pseudanos* Winterbottom 1980 e, mais recentemente, *Petulanos* Sidlauskas & Vari 2008.

O segundo trabalho sobre relações filogenéticas de espécies de Anostomidae foi bem mais recente (Sidlauskas & Vari, 2008), e contém uma hipótese mais abrangente de relações entre todos os gêneros da família, resultado de uma análise de parcimônia com 123 caracteres morfológicos codificados para 46 espécies de Anostomidae (Fig. 1). Um dos fatores limitantes na análise de Sidlauskas & Vari (2008) é a pouca representatividade de espécies, em especial as de *Leporinus*, além de várias espécies examinadas serem exemplares juvenis ou adultos jovens, no qual dúvidas em relação a delimitação de alguns gêneros podem ser geradas, em especial *Hypomasticus* e *Leporinus* (Birindelli & Britski, 2009).

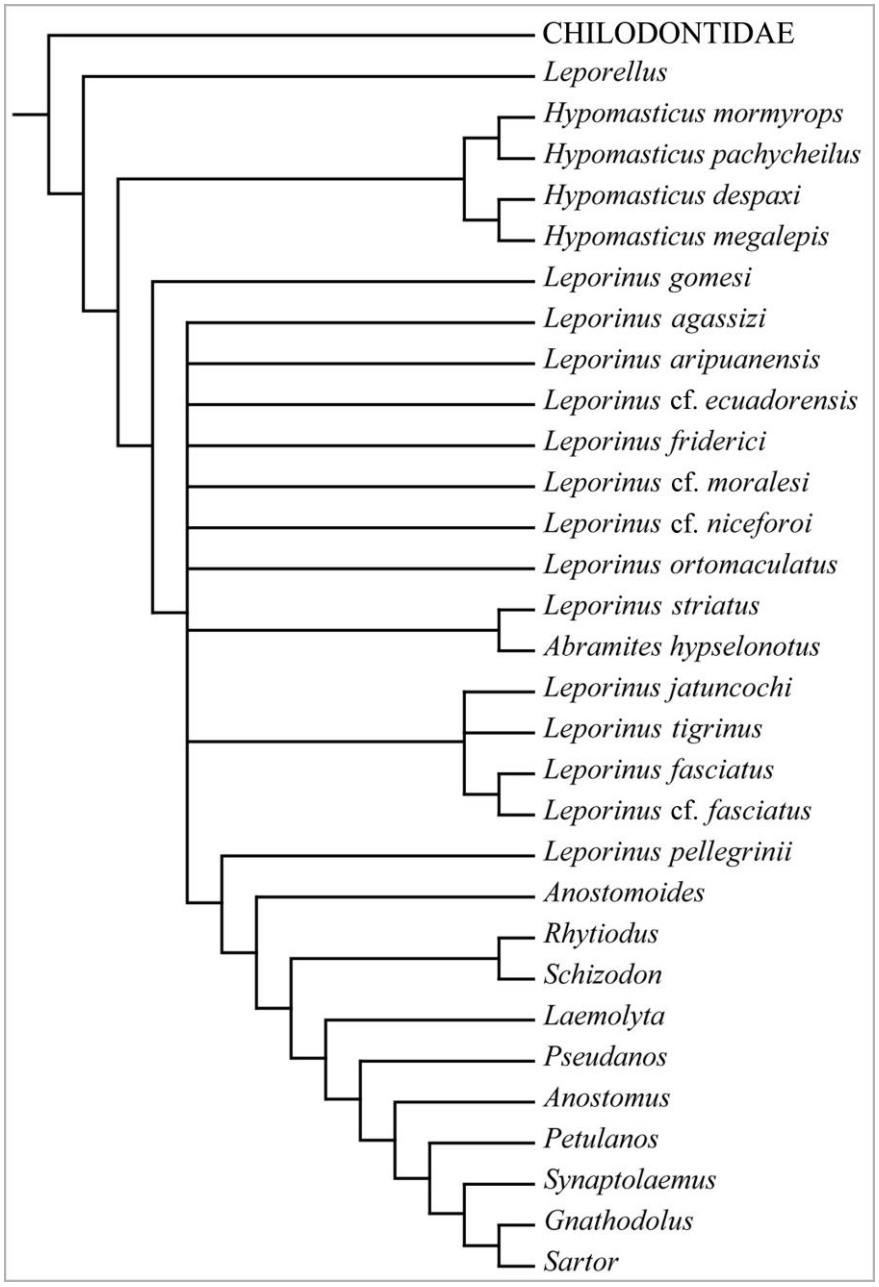


Fig. 1. Cladograma resumido de consenso estrito das relações entre táxons de Anostomidae, segundo a hipótese proposta por Sidlauskas & Vari (2008).

Mais recentemente, estudos que utilizam dados moleculares têm sido realizados (Ramirez, 2015; Ramirez *et al*., 2015, 2016a, 2016b, 2017). Nestes estudos, o polifiletismo de *Leporinus* foi confirmado (Ramirez *et al*., 2016a) e as relações entre as espécies de *Laemolyta* foram estudadas (Ramirez, 2015). Além disso, um novo gênero, *Megaleporinus* Ramirez, Birindelli & Galetti Jr., 2016, foi descrito com base em

caracteres morfológicos, citogenéticos e moleculares, e uma nova hipótese filogenética e biogeográfica proposta para suas 10 espécies (Ramirez *et al*., 2016a). Por outro lado, as novas hipóteses moleculares *(e.g*., Ramirez *et al*., 2016b) têm trazido incrongruências com as hipóteses baseadas em dados morfológicos (*e.g*., Winterbottom, 1980; Sidlauskas & Vari, 2008), principalmente pela posição filogenética de Anostominae, próxima da base da família, juntamente com *Leporellus* (Ramirez *et al*., 2016b).

Revisões taxonômicas foram realizadas em nível de gênero por Vari & Williams (1987) para *Abramites* e por Mautari & Menezes (2006) para *Laemolyta* Cope, 1872. Algumas revisões parciais foram realizadas para os gêneros *Leporinus* Agassiz, 1829 (Géry *et al*., 1988; Garavello, 1990, 2000; Britski, 1997; Britski *et al*., 2012; Birindelli & Britski, 2013) e *Schizodon* Agassiz, 1829 (Bergmann, 1988; Garavello & Britski, 1990). Apesar destes esforços, há ainda alguns gêneros e grupos de espécies cujo conhecimento taxonômico ainda é precário.

Desse modo o presente estudo se insere nesse contexto e tem como objetivo a realização de uma revisão sistemática de *Anostomoides*, que resolva os problemas taxonômicos que tem dificultado a identificação de suas espécies, e investiguem as relações filogenéticas entre as espécies do gênero. Para isso, esta tese foi dividida em dois capítulos, o primeiro focado nas questões taxonômicas, e o segundo voltado a testar o monofiletismo do gênero e as relações filogenéticas de suas espécies.

Referências bibliográficas

Bergmann, L.A.C. (1988) *Schizodon jacuiensis* sp. n., um novo anostomídeo do sul do Brasil e redescrição de *Schizodon kneri* (Steindachner, 1875) e *S. platae* (Garman, 1890). (Pisces, Characiformes, Anostomidae). *Comunicações do Museu de Ciências da PUCRS, Série Zoologia*, 1, 13–28.

Birindelli, J.L.O. & Britski, H.A. (2009) New species of *Leporinus* Agassiz (Characiformes: Anostomidae) from the Rio Curuá, Rio Xingu basin, Serra do Cachimbo, Brazil, with comments on *Leporinus reticulatus*. *Neotropical Ichthyology,* 7(1), 1–10.

Birindelli, J.L.O. & Britski, H.A. (2013) Two new species of (Characiformes: Anostomidae) from the Brazilian Amazon, and redescription of Kner 1858. *Journal of Fish Biology,* 83(5), 1128–1160.

Britski, H.A. (1997) Descrição de duas espécies novas de *Leporinus* dos rios Araguaia e Tocantins, e comentários sobre as demais espécies do gênero assinaladas na bacia

(Ostariophysi, Characiformes, Anostomidae). *Comunicações do Museu de Ciências e Tecnologia da PUCRS, série Zoologia,* 10, 27–43.

Britski, H.A., Birindelli, J.L.O. & Garavello, J.C. (2012) A new species of *Leporinus* Agassiz, 1829 from the upper Rio Paraná basin (Characiformes, Anostomidae) with redescription of *L. elongatus* Valenciennes, 1850 and *L. obtusidens* (Valenciennes, 1837). *Papéis Avulsos de Zoologia (São Paulo)*, 52, 441–475.

Chao, N.L., Petry, P., Prang, G., Sonneschien, L. & Tilusty, M. (2001). *Conservation and Management of Ornamental Fish Resources of the Rio Negro Basin, Amazonia, Brazil – Projeto Piaba*. Editora da Universidade do Amazonas, Manaus, pp.310.

Dillman, C.B., Sidlauskas, B.L., Vari, R.P., 2016. A morphological supermatrix-based phylogeny for the Neotropical fish superfamily Anostomoidea (Ostariophysi: Characiformes): phylogeny, missing data and homoplasy. *Cladistics*. 32, 276–296. http://dx.doi.org/10.1111/cla.12127.

Fricke, R., Eschmeyer, W. N. & R. Van Der Sleen (eds) 2019. CATALOG OF FISHES: GENERA, SPECIES, REFERENCES. (http://researcharchive.calacademy.org/

research/ichthyology/catalog/fishcatmain.asp). Electronic version accessed 28 jan 2019.

Garavello, J.C. (1990) A new species of the anostomid genus *Leporinus* Spix from Suriname, with redescriptions of two related species (Pisces, Characiformes, Anostomidae). *Bulletin Zoologisch Museum*. 12(11), 161–70.

Garavello, J.C. (2000) Two new species of *Leporinus* Spix with a review of the blotched species of the río Orinoco system and redescription of *Leporinus muyscorum* Steindachner (Charciformes: Anostomidae). *Proceedings of the Academy of Natural Sciences of Philadelphia.* 193–201.

Garavello, J.C. & Britski, H.A. (1990) Duas novas espécies do gênero *Schizodon* Agassiz da bacia do alto Paraná, Brasil, América do Sul (Ostariophysi, Anostomidae). *Naturalia.* 15,153–70.

Garavello, J.C. & Britski, H.A. (2003) Family Anostomidae. *In:* Reis, R.E., S.O. Kullander & C.J. Ferraris (Eds.), *Check list of the freshwater fishes of South and Central America*. Edipucrs, Porto Alegre, pp. 71–84.

Géry, J. (1977) *Characoids of the world*. T. F. H. Publications, Neptune City, New Jersey, 672 pp.

Géry, J., Planquette, P. &, Le Bail, P.Y. (1988) Nomenclature des espèces du groupe Leporinus maculatus et formes affines des Guyanes (Pisces: Characoidei: Anostomidae). *Revue suisse de Zoologie*. 95(3), 699–713.

Mautari, K.C. & Menezes, N.A. (2006) Revision of the South American freshwater fish genus *Laemolyta* Cope, 1872 (Ostariophysi, Characiformes, Anostomidae). *Neotropical Ichthyology*, 4(1), 27–44.

Mirande, J.M. (2018) Morphology, molecules and the phylogeny of Characidae (Teleostei, Characiformes). *Cladistics*, 1–9. https://doi.org/10.1111/cla.12345

Ramirez, J.L. (2015) Filogenia molecular dos Anostomidae e filogeografia das espécies com cromossomos sexuais ZZ/ZW do gênero *Leporinus*. Universidade Federal de São Carlos, Centro de Ciências Biológicas e da Saúde, São Carlos, 150 pp.

Ramirez, J.L., Birindelli, J.L.O. & Galetti, P.M. (2016a) A New Genus of Anostomidae (Ostariophysi: Characiformes): Diversity, Phylogeny and Biogeography Based on Cytogenetic, Molecular and Morphological Data. *Molecular Phylogenetics and Evolution*, 107, 308–323.

Ramirez, J.L., Carvalho-Costa, L.F., Venere, P.C., Carvalho, D.C., Troy, W.P., Galetti, P.M. (2016b). Testing monophyly of the freshwater fish *Leporinus* (Characiformes, Anostomidae) through molecular analysis. *Journal Fish Biology*, 88, 1204–1214.

Ramirez, J.L., Birindelli, J.L.O., Carvalho, D.C., Affonso, P.A.M., Venere, P.C., Ortega, H., Carrillo-Avila, M., Rodríguez-Pulido, J.A. & Galetti, P.M.. (2017) Revealing Hidden Diversity of the Underestimated Neotropical Ichthyofauna: DNA Barcoding in the Recently Described Genus *Megaleporinus* (Characiformes: Anostomidae). *Frontiers in Genetics*, 8, pp. 149.

Sidlauskas, B. & Vari, R.P. (2008) Phylogenetic relationships within the South American fish family Anostomidae (Teleostei, Ostariophysi, Characiformes). *Zoological Journal of the Linnean Society,* 154(1), 70–210.

Van Der Sleen, P. & Alberts, J.S (2018) *Field Guide to the Fishes of the Amazon, Orinoco, and Guianas*. Princeton: Princeton University Press, pp. 464.

Vari, R.P. (1983). Phylogenetic relationships of the Families Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae (Pisces, Characiformes). *Smithsonian Contributions to Zoology*, 378, 1–60.

Vari, R.P. & Williams, A.M. (1987) Headstanders of the Neotropical anostomid genus *Abramites* (Pisces: Characiformes: Anostomidae). *Proceedings of the Biological Society of Washington*, 100(1), 89–103.

Winterbottom, R. (1980) Systematics, osteology and phylogenetic relationships of fishes of the ostariophysan subfamily Anostominae (Characoidei, Anostomidae). *Life Sciences Contributions: Royal Ontario Museum*, 123, 1–112.

- Capítulo 1 -

Taxonomic revision of the genus *Anostomoides* (Characiformes: Anostomidae)

Artigo formatado nas normas da Revista Zootaxa

Taxonomic revision of the genus *Anostomoides* (Characiformes: Anostomidae)

FERNANDO MASSAYUKI ASSEGA[1,2] & JOSÉ LUÍS OLIVAN BIRINDELLI[1]

[1] *Programa de Pós-Graduação em Ciências Biológicas, Universidade Estadual de Londrina, Centro de Ciências Biológicas, Rodovia Celso Garcia Cid, Campus Universitário, 86057-970, Londrina-PR, Brazil. E–mail: (FMA) fernandoassega@hotmail.com; (JLOB) josebirindelli@yahoo.com*

[2] *Corresponding author. E–mail: fernandoassega@hotmail.com*

Abstract

The genus *Anostomoides* currently includes three valid species: *A. atrianalis* (described for the Orinoco basin), *A. laticeps* (reported from the Amazon and Essequibo basins), and *A. passionis* (reported from the Rio Xingu and Rio Tapajós basins). The first two species were described a long time ago, whereas *A. atrianalis* remained poorly known until now, and the latter was recently described based on a relatively small sample of specimens from a restricted area. In addition, an ongoing taxonomic revision of the species of *Leporinus* discovered that *L. nattereri* possibly belonged to *Anostomoides*. The present study aimed a taxonomic revision of *Anostomoides* based on morphometric and meristic data, and a comprehensive revision of the literature and specimens deposited in fish collections. Examining 274 specimens, the present taxonomic revisionew demonstrates that *A. laticeps* is a junior synonym of *A. atrianalis*, while *A. passionis* is a junior synonym of *Leporinus nattereri*, and the latter name is thus transferred to *Anostomoides* forming the new combination: *Anostomoides nattereri*. Principal components analysis (PCA) showed that examined specimens form two distinct morphotypes, corroborating the validity of both *A. atrianalis* and *A. nattereri*. *Anostomoides nattereri* is distinguished from *A. atrianalis* by having four branchiostegal rays (*vs.* three), three pores in infraorbital one (*vs.* four), 37–39 pored lateral-line scales (*vs.* 41–44), symphyseal tooth of premaxillary blunt cutting edge (*vs.* bicuspid), lower lip with dermal papillae (*vs.* absent), three dark rounded midlateral blotches (vs. three or four vertically elongated blotches and/or a faded dark longitudinal stripe), dark lines between scale series on posterior half of body on specimens smaller than 150 mm SL (*vs.* dark lines absent), a greater body depth (27.6–36.2 % *vs*. 24.5–38.7% of SL) and smaller interorbital distance (34.4–53.8 % *vs.* 42.6–67.3 % of HL). *Anostomoides nattereri* is distributed across several tributaries of the Amazon river, including the Negro, Tapajós, Xingu and Tocantins rivers, whereas *A. atrianalis* is widespread throughout the Amazon, Orinoco and Essequibo basins. The genus *Anostomoides* is currently diagnosed based on a combination non-exclusive characters: upturned or slightly upturned mouth with four premaxillary teeth including symphyseal tooth bicuspid or with blunt cutting edge, remaining teeth slightly tricuspid (with medial cuspid distinctly larger); four dentary teeth, symphyseal tooth with truncate cutting edge (without cusps); second tooth with a single large cusp, and two lateral teeth with small cusps (three or slightly more cusps).

Keywords: Systematics, South America, *Anostomoides atrianalis*, *Anostomoides nattereri*

Resumo
O gênero *Anostomoides* atualmente possui três espécies válidas: *A. atrianalis* (descrita para a bacia do Orinoco), *A. laticeps* (bacia dos rios Amazônia e Essequibo) e *A. passionis* (bacia dos rios Xingu e Tapajós). As duas primeiras espécies foram descritas há muitos anos, *A. atrianalis* permaneceu pouca conhecida até o momento, e *A. passionis* foi descrita recentemente com base em uma amostra relativamente pequena de espécimes de uma área restrita. Além disso, uma revisão taxonômica das espécies de *Leporinus* que está em andamento, revelou que *L. nattereri* possivelmente pertencia ao gênero *Anostomoides*. O objetivo do presente estudo foi realizar uma revisão taxonômica do gênero baseada em dados morfométricos e merísticos e uma abrangente revisão da literatura e dos espécimes presentes nas coleções de peixes. Examinando 274 espécimes, a revisão taxonômica demonstrou que *A. laticeps* é sinônimo júnior de *A. atrianalis*, enquanto que *A. passionis* é sinônimo júnior de *Leporinus nattereri*, sendo o último nome então transferido para *Anostomoides* formando a nova combinação: *Anostomoides nattereri*. A análise de componentes principais (PCA) mostrou que os espécimes examinados formam dois morfotipos distintos, corroborando a validade tanto de *A. atrianalis* quanto de *A. nattereri*. *Anostomoides nattereri* distingue-se de *A. atrianalis* por ter quatro raios branquiostégios (*vs.* três), três poros no infraorbital 1 (*vs.* quatro), 37–39 escamas na linha lateral (*vs.* 41–44), dente sinfisiano do premaxilar truncado (*vs.* bicuspidado), lábio inferior com papilas dérmicas (vs. ausentes), três manchas arredondadas escuras na lateral do corpo (contra três ou quatro manchas alongadas verticalmente e/ou uma faixa longitudinal escura desbotada), linhas escuras entre as séries de escamas na metade posterior do corpo em espécimes menores que 150 mm CP (*vs.* linhas escuras ausentes), maior altura do corpo (27,6–36,2% *vs*. 24,5–38,7% do CP e menor distância interorbital (34,4–53,8% *vs.* 42,6–67,3% do CC). *Anostomoides nattereri* está distribuído em vários afluentes do Rio Amazonas, incluindo os rios Negro, Tapajós, Xingu e Tocantins, enquanto o *A. atrianalis* é difundido em todas as bacias do Amazonas, Orinoco e Essequibo. O gênero *Anostomoides* é atualmente diagnosticado com base em uma combinação de caracteres não exclusivos: boca superior ou ligeiramente superior com quatro dentes no pré-maxilar, incluindo o dente sinfisiano bicuspidado ou truncado (sem cúspides), e os dentes remanescentes levemente tricúspides (com cúspide medial distintamente maior); quatro dentes presente no dentário, o dente sinfisiano truncado; o segundo dente com uma única cúspide grande e os outros dois dentes laterais com pequenas cúspides (três ou mais cúspides).

Palavras-chave: Sistemática, América do Sul, *Anostomoides atrianalis*, *Anostomoides nattereri*

Introduction

The family Anostomidae is currently composed of 145 valid species, distributed in 15 genera (Ramirez *et al*., 2017). The family is endemic to the Neotropical region, and widely distributed from north of the Colombia to La Plata river, in Argentina (Garavello & Britski, 2003). The Anostomidae can be easily diagnosed by their dentition, which almost always consists of three or four large teeth arranged in a single row on each side of the upper and lower jaws (Sidlauskas & Birindelli, 2017).

Approximately more than half of the species of Anostomidae are currently placed in the artificial genus *Leporinus*. On the other hand, most genera are monotypic (*e.g*., *Gnathodolus*) or composed by a handful of species (*e.g*., *Petulanos*). This is also the case of *Anostomoides*, currently considered as presenting only three valid species: *A. atrianalis*, recorded only from the Orinoco river in Venezuela; *A. laticeps*, considered to have a wide distribution in the Amazon, and Essequibo basins, and *A. passionis,* a species possibly endemic to the Volta Grande rapids of the Xingu river in Brazil (Garavello & Britski, 2003; Santos & Zuanon, 2006).

The taxonomic history of the genus *Anostomoides* started between the years of 1885 and 1886, when the French naturalist Jean Chaffanjon lead an expedition to the Orinoco river basin in Venezuela (Rodriguez, 1993), during which three specimens of Anostomidae with a slightly upturned mouth were collected. The specimens were described by Pellegrin (1909) as a new genus and species: *Anostomoides atrianalis* Pellegrin. According to Pelegrin (1909), *Anostomoides* is likely a species intermediary between the genera *Leporinus* and *Anostomus*.

A few years later, Eigenmann (1912) described *Schizodontopsis laticeps* (= *Anostomoides laticeps*) based on four specimens collected in the Essequibo river in Guyana. These two species of *Anostomoides* remained known only from their types for many decades.

Borodin (1931) in a review of the genus *Anostomus* include *Anostomoides laticeps* to the subgenus *Schizodontopsis Garman*, 1890, presenting as its type species *Anostomus proximus* Borodin, 1890 (= *Laemolyta proxima*), and considered *Anostomoides* as a subgenus of *Schizodontopsis*. Myers (1950) reviewed the genera of Anostomidae and recognized *Schizodontopsis* as a junior synonym of *Laemolyt*a Cope, 1872, and transferred *Schizodontopsis* (*Anostomoides*) *laticeps* to *Laemolyta laticeps*. Myers (1950) considered the monotypic genus *Anostomoides* a taxon with insufficient information to determine its validity. Later, Géry (1974), in a footnote, transferred *L.*

laticeps back to *Anostomoides* revalidating the genus. In 1977, Géry, included *Anostomoides* in a species identification key for Anostomidae where the genus was diagnosed by the presence of more or less supraterminal mouth, 3 or 4 rounded teeth on each jaw, pre-maxillary teeth sometimes tricuspid and relatively high body. More recently, Santos & Zuanon (2006) described *Anostomoides passionis*, a species apparently endemic from the Volta Grande rapids of the middle Xingu river in Brazil.

The phylogenetic relationships of *Anostomoides* are also insufficiently studied. Sidlauskas & Vari (2008) recovered *Anostomoides laticeps* as sister group to Anostominae (*Anostomus, Gnathodolus, Petulanos, Pseudanos, Sartor* and *Synaptolaemus*) plus *Laemolyta*, *Rhytiodus*, and *Schizodon*, in a comprehensive analysis based on morphological features. However, molecular-based analyses have showed that the Anostominae is more likely sister to *Leporellus*, whereas *Anostomoides laticeps*, *Laemolyta, Rhytiodus*, *Schizodon* are closely related (Melo, 2015; Ramirez, 2015).

Species of *Anostomoides* are mentioned only sporadically in field guides and local checklists (*e.g.* Feitosa & Santos, 2013; Ohara *et al.*, 2017). The genus, as well as its species, remains poorly diagnosed. In addition, the scarcity of published information about the anatomy as well as molecular data of *Anostomoides* species increases the difficulty in establishing a relationship among the genus and others anostomids. Therefore, a taxonomic revision is imperative to determine the validity and geographical distribution of each of the nominal species of *Anostomoides*, a prerequisite to understand the evolutionary history of its species.

During an ongoing taxonomic revision of all nominal species of *Leporinus*, the type specimens of *Leporinus nattereri* were examined and the species was considered possibly closely related to *Anostomoides passionis* (JLB, pers. obs.). Later examination of more recently collected specimens confirmed this first impression. Therefore, *L. nattereri* was included in the present study and is evaluated herein. *Leporinus nattereri* was described by Steindachner (1876) based on specimens collected in the Amazon. Simlarly to the nominal species of *Anostomoides*, *Leporinus nattereri* remained poorly known until now.

The present study aimed a comprehensive taxonomic revision of *Anostomoides*, determining its valid species, and their geographic distributions.

Material and methods

A total 274 of specimens belonging to *Anostomoides* were examined. Type specimens were directly examined (*A. laticeps*, *A. passionis* and *L. nattereri*) or through photographs (*A. atrianalis*). Institutional and collections abbreviations follow Sabaj (2016).

Measurements were taken following Sidlauskas *et al.* (2011). Morphometric data were obtained with a digital caliper with accuracy of 0.01 mm. Counts of scales and rays were taken according to Birindelli & Britski (2013). Meristic data were included in the description of each species, with frequency of each count provided in parentheses, and an asterisk (*) indicating the values of the primary types.

Differences in body shape among samples, and discriminat characters between specimens were determined by principal components analysis (PCA) using the PAST software (Hammer *et al*., 2003). Data were normalized to size and log transformed to produce a scatter plot of specimens along the axes two and three, producing maximal and second to maximal separation between all groups. Samples were identified according to the species concepts prior to the results herein obtained to test the validity of these concepts: *Anostomoides atrianalis* (Orinoco basin), *Anostomoides laticeps* (Amazon and Essequibo basins), *Anostomoides passionis* (Rio Xingu basin), and *Leporinus nattereri* (Amazon basin, except Rio Xingu basin).

Cleared and double stained (cs) specimens were prepared following Taylor & Van Dyke (1985), and dry skeletons (sk) according to Bemis *et al*. (2004). Specimens were dissected using the technique described in Weitzman (1974). Osteological nomenclature follows Weitzman (1962), Winterbottom (1980), and Sidlauskas & Vari (2008).

Results

The analysis of morphological and meristic data undertaken in the present study, allowed the recognition of only two valid species of *Anostomoides*: *A. atrianalis* (Amazon, Essequibo and Orinoco basins) and *A. nattereri* (Amazon basin, including the Negro, Tapajós, Xingu, and Tocantins rivers). Herein we consider *Anostomoides laticeps* a junior synonym of *A. atrianalis*, and *A. passionis* a junior synoym of *Leporinus nattereri*, which was consequently transferred to *Anostomoides* in a new combination.

Morphological analysis

In principal components analysis (PCA), the second and third axis showed better separation of the combined samples of *Anostomoides atrianalis* and *A. nattereri*. The second and third axis, represented the shape, showed variation retained 2.788% and 1.162% respectively (Table 1).

TABLE 1. Weight of the variables combined in the Principal Components Analysis (axes 2 and 3) of *Anostomoides atrianalis*, *A. nattereri* (Amazon rivers, except Xingu) and *A. nattereri* (Xingu river).

Morphometrics measures	Axis 2	Axis 3
Adipose-fin origin to hypural joint	-0.132	0.231
Body depth	0.124	-0.203
Body width	0.002	-0.223
Bony interorbital	-0.207	-0.075
Caudal-peduncle depth	0.062	-0.075
Caudal-peduncle length	-0.216	0.070
Dorsal-fin origin to adipose-fin origin	-0.293	-0.028
Dorsal-fin origin to caudal-fin origin	-0.276	0.016
Eye diameter	-0.255	0.119
Head length	0.109	0.207
Head depth	0.201	-0.294
Lower jaw to anal-fin origin	-0.128	0.052
Lower jaw to adipose-fin origin	-0.133	0.022
Lower jaw to dorsal-fin origin	-0.019	0.111
Lower jaw to pectoral-fin origin	0.090	0.273
Lower jaw to pelvic-fin origin	0.020	0.099
Preopercle depth	0.279	-0.313
Preopercle length	0.181	0.207
Standard length	-0.142	0.028
Snout depth	0.334	-0.407
Snout length	0.556	0.537
Eigenvalue	0.007	0.003
% variance	2.788	1.162

Figure 1 showed that samples form two groups, corroborating the morphometric and meristic data, and therefore the validity of *Anostomoides atrianalis* (= *A. atrianalis* plus *A. laticeps*) and *A. nattereri* (= *Leporinus nattereri* plus *A. passionis*). The sample of *A. atrianalis* is distinguished from the sample of *A. nattereri* in the third axis. The morphometric measurements that discriminate *A. atrianalis* from *A. nattereri* are: body depth, body length, head depth, preopercle depth and snout depth (most negative values in the third canonical axis) (Table 1). The superimposed group formed by samples of *A. nattereri* was discriminated from the *A. atrianalis* by: adipose-fin origin to hypural joint, eye diameter, head length, lower jaw to dorsal-fin origin, lower jaw to pectoral-fin origin, lower jaw to pelvic-fin origin, preopercle length and snout length.

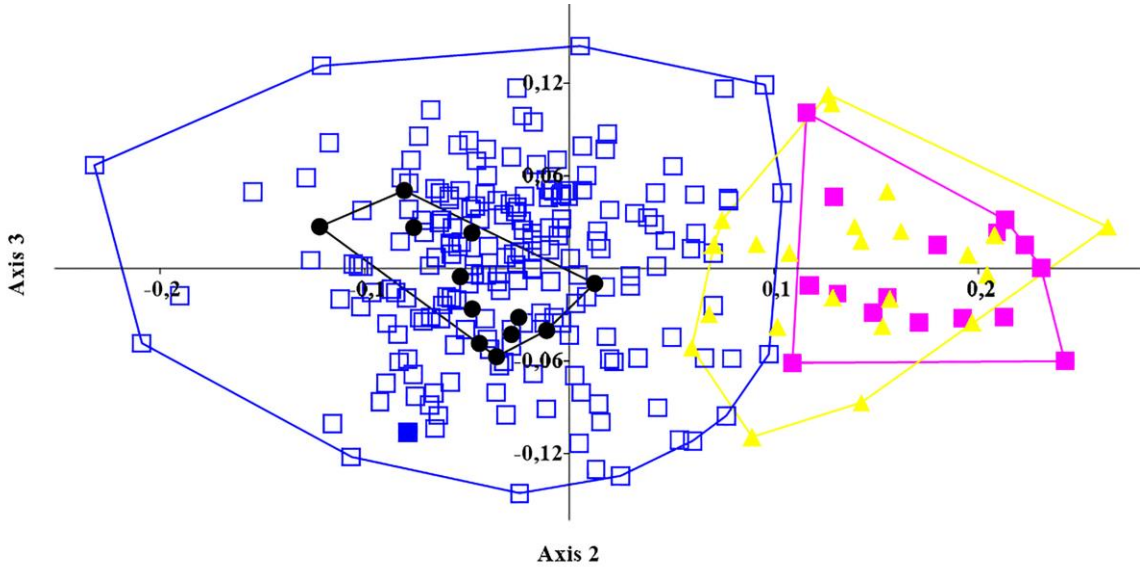


FIGURE 1. Scatter diagram of scores of specimens on second and third axes of Principal Components Analysis (PCA) of *Anostomoides atrianalis* from the Amazon basin (blue square), Essequibo River, Guyana (fill blue square), and Orinoco basin (black dot), *A. nattereri* from the Rio Xingu (yellow triangle), and *A. nattereri* from the remaining Amazon basin (filled pink square).

Redescriptions

Genus *Anostomoides* Pellegrin

Anostomoides Pellegrin 1909: 346. Type species: *Anostomoides atrianalis* Pellegrin 1909. Type by monotypy. Gender: masculine.

Diagnosis. The genus *Anostomoides* is diagnosed among Anostomidae by having the following combination of non-exclusive features: mouth upturned or slightly upturned with four teeth on premaxillary (Figure 2), including symphyseal tooth unicuspid or bicuspid (never tricuspid), remaining teeth slightly tricuspid (with medial cuspid distinctly larger); four dentary teeth, symphyseal tooth with truncate cutting edge (without cusps); second tooth with a single large cusp, and two lateral teeth with small cusps (three or slightly more cusps) (Figure 3); lower jaw lip fringed or fringed with dermal papillae. See Discussion for comparisons with other genera.

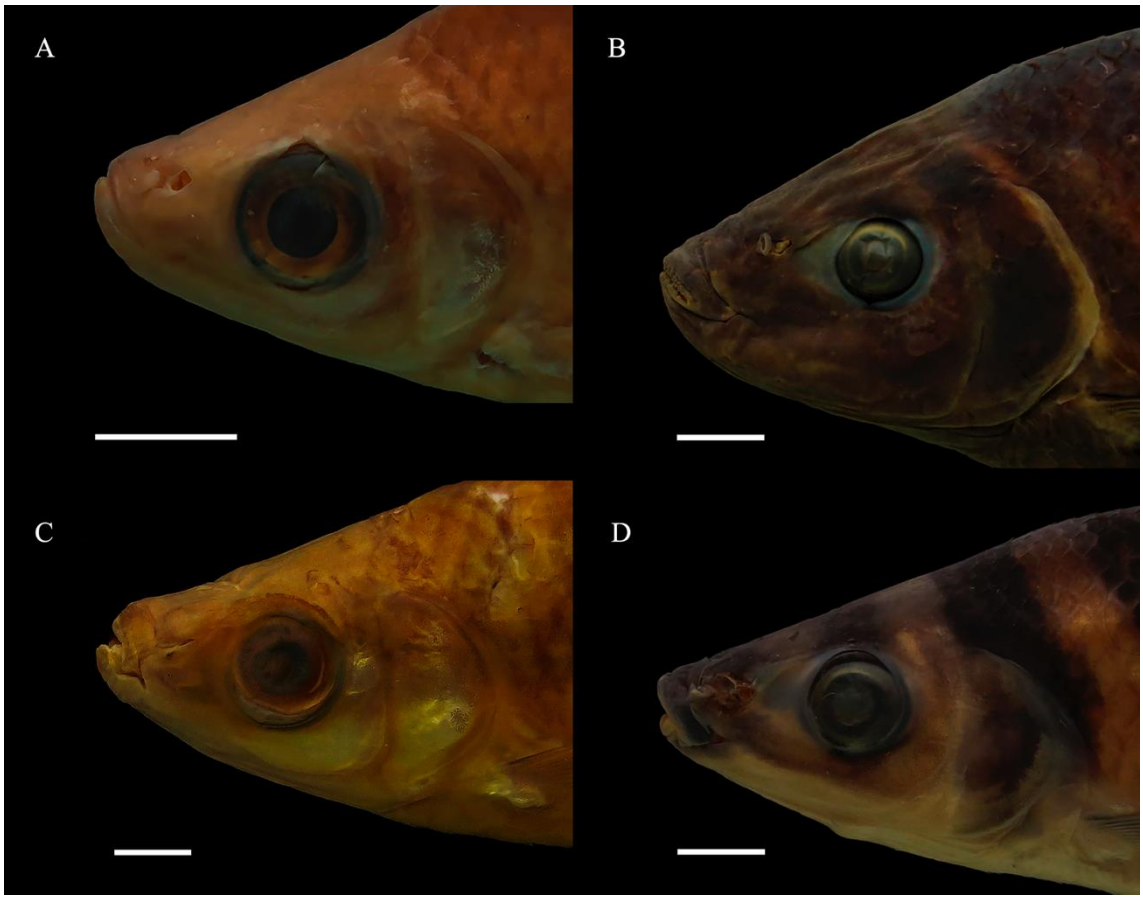


FIGURE 2. Lateral view of head showing the position of the mouth, upturned (A and C), slightly upturned (B) and terminal (D). (A) *Anostomoides atrianalis,* ANSP 182467, 128.3 mm SL, Peru, Loreto, Río Nanay; (B) *A. nattereri*, LIA 1229, 175.5 mm SL, Brazil, Pará, Rio Xingu; (C) *Laemolyta proxima*, MZUEL 17132, 215.5 mm SL, Brazil, Amazonas, Manaus; (D) *Leporinus fasciatus*, MZUEL 14698, 136.3 mm SL, Brazil, Amazonas, Rio Negro. Scale bar = 10 mm.

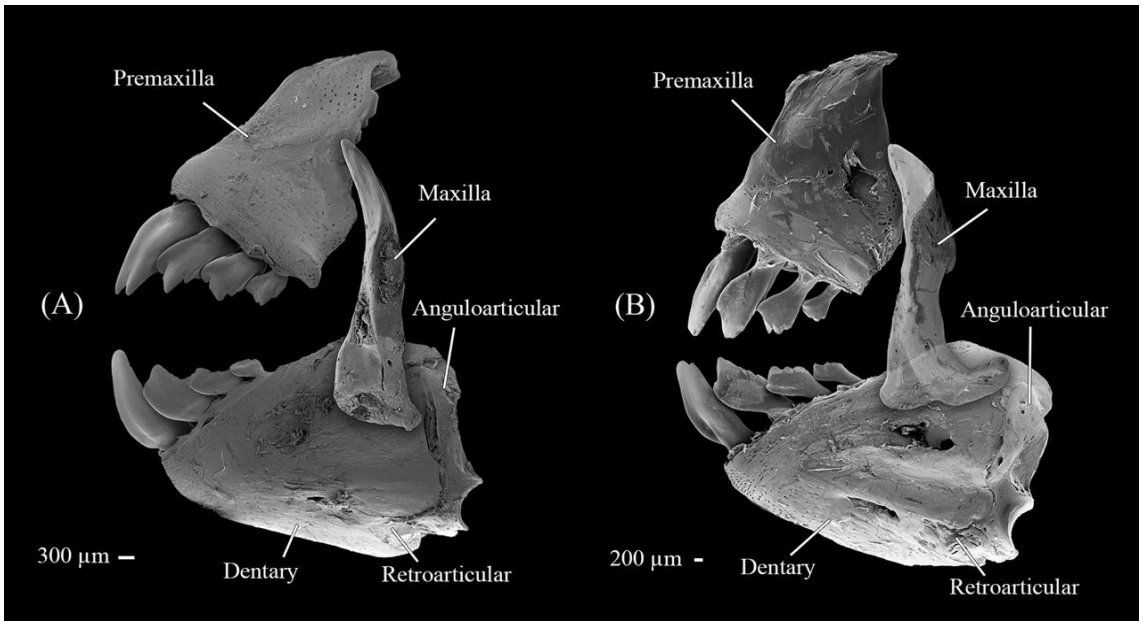


FIGURE 3. Scanning electron microscope image of left upper and lower jaws of *Anostomoides*: (A) *A. atrianalis*, INPA 15193, 137.2 mm SL; (B) *A. nattereri*, MZUSP 5429, 89.0 mm SL.

Distribution. The species of *Anostomoides* are distributed in the Amazon, Essequibo and Orinoco basins and their tributaries, in Brazil, Bolivia, Colombia, Guyana, Peru, and Venezuela.

***Anostomoides atrianalis* Pelegrin, 1909**

(Figures. 1, 2A, 3A, 4 A and B, 5, 6; Tables 1 and 2)

Anostomoides atrianalis Pellegrin, 1909: 346 (type locality: "Orénoque" [Río Orinoco, Venezuela]). – Bertin, 1948: 32 (type catalog). – Myers, 1950: 198 (taxonomic comments on the validity of the genus). – Garavello & Britski, 2003: 72 (listed). – Lasso *et al*., 2004: 105 (literature compilation; Colombia: Río Orinoco basin). – Santos & Zuanon, 2006: 60, 66-67 (diagnosis in key; Venezuela, Río Orinoco). – Sidlauskas & Birindelli, 2017: 85 (Río Orinoco basin).

Schizodontopsis laticeps Eigenmann, 1912: 299, pl. 41, fig. 4 (type locality: Crab Falls, Essequibo river, Guyana).

Anostomus (Schizodontopsis) laticeps. – Borodin, 1931: 45 (cited).

Laemolyta laticeps. – Myers, 1950: 197 (new generic combination).

Anostomoides laticeps. – Géry, 1974: 149 (comments in footnote; new generic combination). – Santos *et al*., 1984: 33, fig. 4, unumbered fig on pag. 71 (brief description, diagnosis in key; photo; lower Rio Tocantins, Brazil). – Santos & Jégu, 1989: 164, fig.; pl.IV, figs. 2-4 and 18 (brief description, diagnosis in key; photo, dentition; lower Rio Tocantins, Brazil). – Santos & Jégu, 1996: 160, fig. 9, tab.1 (brief description, diagnosis in key; Rio Uatumã, Brazil). – Ferreira *et al*., 1998: 63, unumbered fig. on p. 63 (brief description, diagnosis in key, photo; Santarém, Pará, Brazil). – Garavello & Britski, 2003: 72 (listed). – Lasso *et al*., 2004: 105 (literature compilation; Colombia, Río Orinoco basin). – Santos *et al*., 2004: 47, unumbered fig. on p. 47 (brief description, diagnosis in key, photo; lower Rio Tocantins, Brazil). – Santos & Zuanon, 2006: 60, 67 (diagnosis in key; several localities in the Amazon basin, Brazil). – Santos *et al*., 2006: 29, unumbered fig. on p. 29 (brief description, diagnosis in key, photo; Manaus, Amazonas, Brazil). – Sidlauskas & Vari, 2008: 78, figs. 19, 32 and 47. (phylogenetic relationships, illustration of neurocranium, dentition of dentary and basibranchial). – Sidlauskas & Vari, 2012: 75, 78, fig. 77 (comments; Essequibo River, Guyana). – Jegú *et al.*, 2012: 119 (listed, Río Iténez basin, Bolivia and Brazil). – Feitosa & Santos, 2013: 149, unumbered fig. on p. 148 (brief description, diagnosis in key; Rio Madeira basin, Brazil). – Sarmiento *et al.*, 2014: 183 (literature compilation; Bolivia). – Ohara *et al*., 2017: 34, 86, fig. (brief description, photo, diagnosis in key; Rio Teles Pires, Brazil). – Sidlauskas & Birindelli, 2017: 85 (cited).
Anostomoides sp. – Santos *et al*., 2004: 48, fig (brief description, diagnosis in key, photo; lower Rio Tocantins basin, Brazil).

Diagnosis. *Anostomoides atrianalis* differs from *A. nattereri* by having three branchiostegal rays (*vs.* four), four pores in the infraorbital 1 (*vs.* three); symphyseal teeth of premaxillary bicuspid, and remaining teeth slightly tricuspid, with medial cusp distinctly larger, or with blunt cutting edge (*vs.* teeth larger, wider, border slightly convex, and remaining teeth with truncate border and sometimes with small lateral saliencies forming incipient cusps); higher lateral-line scale counts (41–44 *vs.* 37–39); lower jaw lip without dermal papillae (*vs.* lower jaw lip with dermal papillae) (Figure 4); three or four vertically elongated blotches and/or a faded dark longitudinal stripe (*vs.* three dark rounded midlateral blotches), absence of dark lines between scale series on posterior half of body (*vs.* dark lines between scale series on posterior half of body in specimens smaller than 150 mm SL).

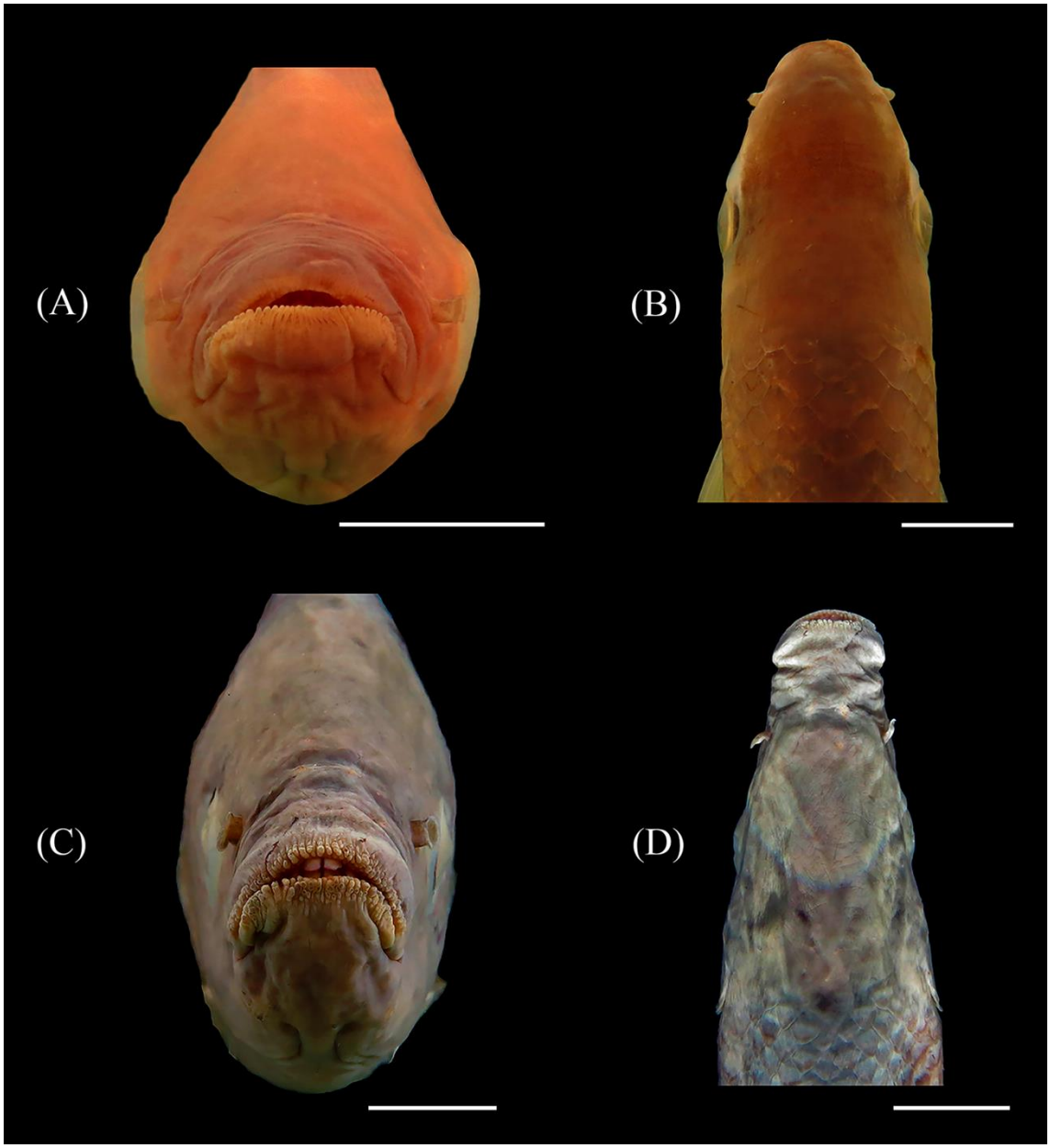


FIGURE 4. *Anostomoides atrianalis*, ANSP 159599, 128.4 mm SL (A and B) and *A. nattereri*, LIA 1229; 175.5 mm SL (C and D), in frontal (A and C) and dorsal (B and D) views from the head showing the lips fringed without dermal papillae (A) or fringed with numerous dermal papillae (C). Scale bar = 10 mm.

Description. Body moderately slender, slightly compressed lateraly, greatest body depth at dorsal-fin origin. Dorsal profile slightly sloped and convex from snout tip to vertical through nostril; slightly concave from vertical through nostril to tip of supraoccipital spine and gently sloped and convex from this point to beginning of

dorsal-fin origin; slightly slanted and convex along dorsal-fin base; approximately straight or slightly convex from end of dorsal fin to adipose-fin origin, and concave from that point to origin of dorsal procurrent caudal-fin rays (Figure 5). Ventral profile slanted convex from tip of lower jaw to vertical through pectoral-fin origin; slightly convex from vertical through pectoral-fin origin to anal-fin origin; approximately straight along anal-fin base, and concave from anal-fin end to origin of ventral procurrent caudal-fin rays; caudal peduncle sligthly compressed, almost rectangular and slightly longer than deep.

Head pointed in profile; snout moderately long. Mouth slightly upturned; lips thick and fleshy, covered internally with numerous papillae. Four premaxillary teeth, symphyseal teeth bicuspid, remaining teeth slightly tricuspid, with medial cusp distinctly larger, or with blunt cutting edge. Four dentary teeth, two medial teeth with truncate cutting edge without cusps, two lateral teeth with three to five small cusps. Lower jaw lips thick and fringed. Three branchiostegal rays.

Scales relatively small and cycloid; lateral line complete, with 41(3), 42(158)*, 43(49) or 44(1) perforated scales, extending from supracleithrum to base of middle caudal-fin rays. Horizontal scale rows between dorsal-fin origin and lateral line 5(8), 6(177), 7(21)* or 8(6). Horizontal scale rows between lateral line and pelvic-fin origin 4(2), 5(193)*, 6(15) or 7(2). Horizontal scale rows between lateral line and anal-fin origin 4(4), 5(193)* or 6(15). Horizontal scale rows around caudal peduncle 16(212)*. Predorsal scales from dorsal-fin origin to tip of supraoccipital spine 10(1), 11(1), 12(13), 13(44), 14(70)*, 15(52), 16(15), 17(8), 18(3), 19(3) or 20(2).

Dorsal-fin rays ii, 9(3) or 10(209)*. Dorsal-fin origin slightly anterior to middle of standard length and slightly anterior to vertical through pelvic-fin origin; distal margin of dorsal fin straight or gently concave. Adipose fin small, approximately rectangular shaped, its origin approximately at vertical through half anal-fin base length, its distal margin slightly convex. Pectoral-fin rays i, 13(3), 14(54)*, 15(154) or 16 (1); its tip extending approximately 3/4 distance between origins of pectoral and pelvic fins; its distal margin slightly convex. Anal-fin rays ii, 7(1), ii, 8(3), iii, 7(1) or iii, 8(207)*; fin origin approximately at vertical through fourth scale anterior to adipose-fin origin; when adpressed anal fin not reaching base of caudal-fin rays; distal margin slightly concave. Principal caudal-fin rays i, 9+8, i (212)*. Caudal fin forked, lobes rounded, upper lobe slightly longer than lower lobe.

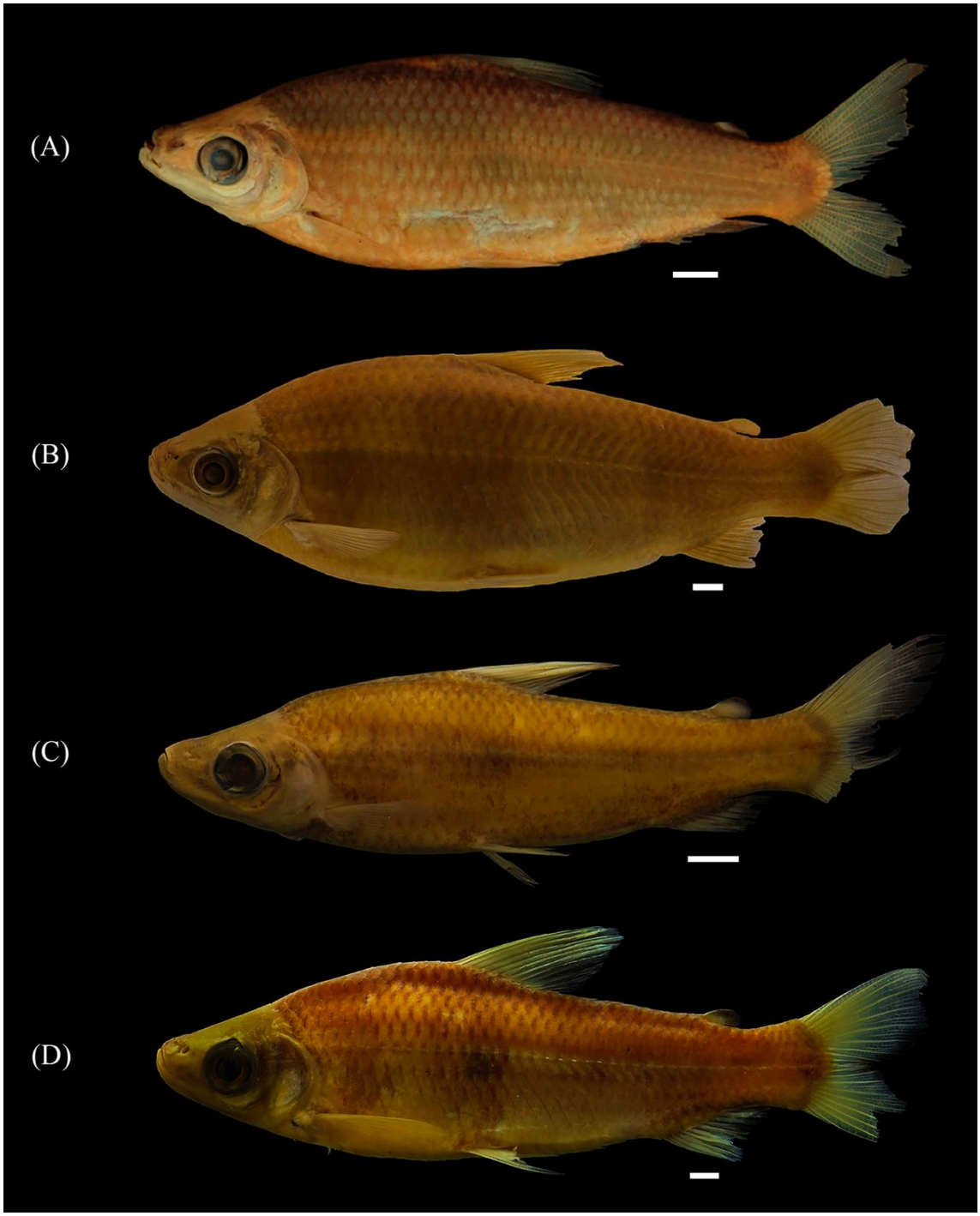


FIGURE 5. *Anostomoides atrianalis*: (A) lectotype, MNHN-IC 1887-0761, 161.7 mm SL, Venezuela, Río Orinoco; (B) holotype of *A. laticeps*, FMNH 53359, 232.5 mm SL, Guyana, Crab Falls, Essequibo River; (C) AUM 43096, 140.4 mm SL, Venezuela, Río Orinoco; (D) ANSP 182467, 126.3 mm SL, Peru, Río Nanay. Scale bars = 10 mm.

TABLE 2. Morphometrics of *Anostomoides atrianalis.* N = Number of specimens, Min = Minimum, Max = maximum, Mean = average, SD = standard deviation.

Character	Lectotype	N	Min–Max	Mean	SD
Standard length (mm)	161.7	208	81.6–266.3	197.2	39.1
Percents of standard length					
Adipose-fin origin to hypural joint	16.7	208	11.9–20.6	17.1	1.3
Body depth	31.8	208	24.5–38.7	30.0	2.3
Body width	13.4	208	9.4–17.4	11.7	1.0
Caudal-peduncle depth	10.5	208	9.3–13.6	10.9	0.6
Caudal-peduncle length	14.3	208	11.4–17.1	14.2	1.1
Dorsal-fin origin to adipose-fin origin	36.8	208	37.2–52.1	42.1	2.1
Dorsal-fin origin to caudal-fin origin	52.9	208	41.2–70.8	57.7	3.4
Head length	23.9	208	19.7–30.3	23.4	1.7
Lower jaw to adiposa-fin origin	82.1	208	79.0–104.9	84.0	2.5
Lower jaw to anal-fin origin	76.1	208	74.6–98.4	78.4	2.2
Lower jaw to dorsal-fin origin	46.2	208	38.9–57.1	43.9	2.3
Lower jaw to pectoral-fin origin	23.2	208	18.0–29.4	22.7	1.9
Lower jaw to pelvic-fin origin	46.5	208	42.9–61.5	47.4	2.1
Percents of head length					
Bony interorbital	54.6	208	42.6–67.3	53.9	3.9
Eye diameter	30.2	208	22.0–39.5	29.4	2.4
Head depth	96.9	208	80.1–132.9	104.9	10.9
Preopercle depth	63.3	208	66.8–119.8	87.2	9.2
Preopercle length	19.0	208	64.0–100.6	73.7	4.4
Snout depth	53.1	208	34.4–90.4	56.3	6.8
Snout length	36.6	208	25.0–44.1	34.3	3.3

Coloration in alcohol. Body with background color light brown. Body sides with three or four vertically elongated blotches: first blotch between opercular opening and vertical through dorsal-fin origin; second blotch below dorsal-fin base; third blotch above anal-fin origin; and the fourth blotch on posterior of caudal peduncle. Faded dark longitudinal stripe present in some specimens. Dorsal fin slightly dark at base, interradial membranes pale on proximal region, and light dark on distal area. Caudal,

pectoral and pelvic fins uniformly tan. Anal fin with rays and interradial membranes dark. Adipose fin light brown, except median portion, which is pale.

Distribution. *Anostomoides atrianalis* is distributed in the Río Orinoco basin in Venezuela, in the Essequibo River basin in Guyana, and in the Amazon basin, including Madeira, Negro, Tocantins and Xingu rivers, in Bolivia, Brazil, Colombia, and Peru (Figure 6).

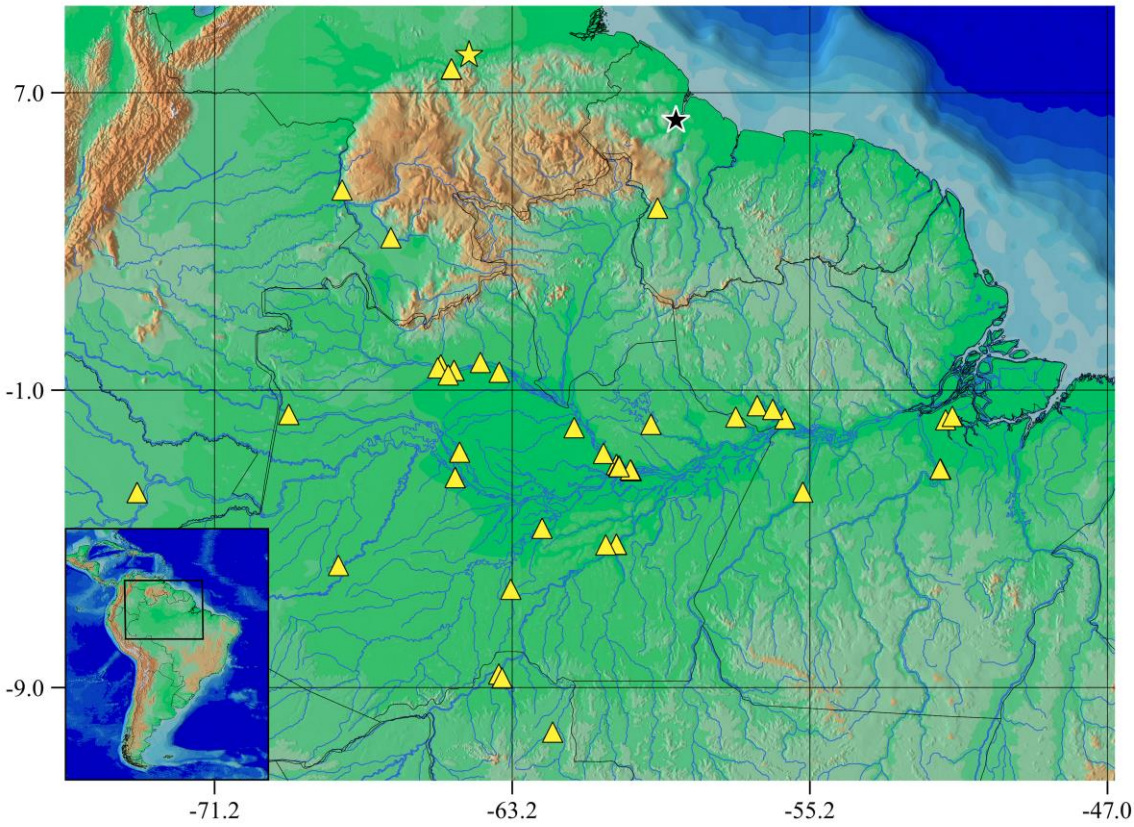


FIGURE 6. Geographic distribution of species of *Anostomoides atrianalis:* yellow star: type-locality of *A. atrianalis*; black star: type-locality of *A. laticeps;* and yellow triangle: records of *A. atrianalis.* Some symbols may correspond to more than one locality.

Remarks. The three syntypes of *Anostomoides atrianalis* were examined through photographs. Two specimens are relatively small and poorly preserved (MNHN 1887-1897 and MNHN 1887-1799), whereas the third specimen is larger and better preserved (MNHN 1887-0761) and, for these reasons, it is herein selected as the lectotype.

The types of *Anostomoides laticeps*, junior synonym of *A. atrianalis*, were deposited in Indiana University. However, in 1952, the Field Museum in Chicago

acquired part of the fish collection of Indiana University. In this exchange, two paratypes of *A. laticeps* (CAS-IU 12116) were lost, as reported in Henn (1928) and Ibarra & Stewart (1987).

Specimens of *Anostomoides atrianalis* are often misidentified as *Laemolyta* in fish collections (Mautari & Menezes, 2006; pers. obs.). Mautari & Menezes (2006) noted that *Anostomoides atrianalis* and *Laemolyta fernandezi* share a similar color pattern and an upturned mouth, and co-occur in the Amazon basin. However, these species differ in the number of lateral-line scales (41 to 44 *vs.* 49 to 58, respectively) and in the morphology of the premaxillary teeth (symphyseal tooth bicuspid, and remaining teeth slightly tricuspid with medial cusp distinctly larger or with blunt cutting edge *vs.* all teeth multicupids and gradually decreasing in size, respectively), and dentary teeth (symphyseal tooth with truncate cutting edge without cusps, and two lateral teeth with three to five small cusps, *vs.* all teeth of the dentary spatulated with the upper edge straight, respectively).

Material Examined. Type material: MNHN-IC 1887-0761, 1, 161.7 mm SL, Venezuela, río Orinoco, J. Chaffanjon, 1887, lectotype of *Anostomoides atrianalis*, by present designation. MNHN-IC 1887-0798, 1, 101.0 mm Sl; MNHN-IC 1887-0799, 1, 92.2 mm SL, Río Orinoco, Venezuela; J. Chaffanjon, 1887. FMNH 53359, 1, 232.5 mm SL, Guyana, Crab Falls, Essequibo river; C.H. Eigenmann, 1908, holotype of *Schizodontopsis laticeps*.

Non-types. Brasil: Amazonas: MZUSP 67267, 1, 235.7 mm SL, Rio Arirará, Igapó (00°31'00" S, 63°33'00" W), M. Goulding, 28 May 1979; MZUSP 31065, 1, 109.0 mm SL; MZUSP 67269, 40, 202.3–260.9 mm SL; MZUSP 109984, 1, 111.9 mm SL, Barcelos, Rio Negro, just below the Rio Daraá (00°28'00" S, 64º46'00" W), M. Goulding, 16 February 1980; MZUSP 67266, 2, 206.7–228.3 mm SL, ilha Mari-Mari, Rio Negro, Igapó Água Preta, M. Goulding, 31 May 1979; MZUSP 6190, 1, 218.7 mm SL, Manaus, Igarapé Jaraqui, left margin of the Rio Negro (03º 00' S, 60º 24'W), Expedição Permanente à Amazônia, 22–24 April 1967; MZUSP 6148, 2, 220.9–223.3 mm SL, Manaus, Rio Negro (03º 00' S, 60º 00' W), 22–25 April 1967; MZUSP 6704, 1, 184.8 mm SL, Manaus, Rio Negro (03°10' S, 60°00'), Expedição Permanente à Amazônia, 15–23 November 1967; INPA 1189, 1, 211.7 mm SL; Manaus, Rio Negro, Lago Tupé (03º 03'30" S, 60º 19' 44" W), G.M. Santos, 20 July 1979; INPA 1191, 2,

210.5–213.3 mm SL, same locality as INPA1189, G.M. Santos, 27 June 1980; INPA 1192, 1, 229.0 mm SL, same locality as INPA1189, G.M. Santos, 22 August 1979; INPA 1188, 3, 151.2–178.4 mm SL, same locality as INPA1189, G.M. Santos, 31 August 1980; INPA 1187, 6, 179.4–206.8 mm SL, same locality as INPA 1189, G.M. Santos, 25 September 1979; INPA 1190, 5, 190.8–206.4 mm SL; INPA 13443, 3, 191.5–209.2 mm SL, Manaus, Rio Negro, pesqueiro do Testa (03º08'30" S, 60º01'28" W), M.L.B. Ribeiro, 31 July 1979; MZUSP 32421, 2, 228.6–266.3 mm SL, Rio Marauiá, cachoeira do Bicho-açu (00°19'00" S, 65° 07'00" W), M.Goulding, 14 October 1979; MZUSP 67268, 2, 214.3–218.4 mm SL, Rio Marauiá (00°24'00" S, 65° 12'00" W), M.Goulding, 14 October 1979; MZUSP 91435, 1, 226.0 mm SL, Rio Negro, Tapera (00°12'00" S, 64°04'00" W), Expedição Permanente à Amazônia, 02 November 1972; INPA 37863, 1, 233.6 mm SL, Santa Isabel do Rio Negro, Rio Aiuanã (00°35'24" S, 64°55'10"W), R. Rayla & P.M. Ito, 03 April 2012; INPA 35580, 1, 202.2 mm SL, Novo Airão, Rio Carabinani (02°00'27" S, 61°32'13" W), R. Silva, N. Ataide & A. Anicacio, 01 December 2008; INPA 9998, 1, 120.0 mm SL, Novo Airão, Rio Jaú, Igarapé do Preto, M. Garcia, 17 July 1993; INPA 13140, 1, 229.4 mm SL, Novo Airão, Rio Jaú, near its mouth (01°53'54" S, 61°26'43" W), Equipe Ictiologia INPA, 26 June 1994; INPA 11746, 1, 163.8 mm SL, Novo Airão, Rio Jaú, M.Garcia & E.Ferreira, 13 June 1995; MZUSP 67264, 5, 188.0–241.0 mm SL, Novo Airão, Rio Negro, Parque Nacional de Anavilhanas, Igapó Estreito (02°42' S, 60°45' W), M. Goulding, August 1980; INPA 11904, 2, 186.2–235.7 mm SL, Novo Airão, Rio Negro, Igarapé Preto (01°46'46" S, 61°45'34" W), M. Garcia, 16 July 1993; INPA 25087, 1, 227.1 mm SL, Novo Aripuanã, Rio Aripuanã, Igarapé Arauazinho (05°09'41" S, 60°41'14" W), L.Rapp Py-Daniel, 28 April 2005; UFRO-ICT 8702, 1, 177.4 mm SL, Novo Aripuanã, Rio Aripuanã, near the mouth of the Rio Madeira (05°08'30.5" S, 60°24'3.3" W), A. Ribeiro, 05 December 2008; UFRO-ICT 1832, 1, 152.1 mm SL, Novo Aripuanã, Rio Aripuanã (05°08'55.7" S, 60°23'50.3" W), F. Viana, 22 January 2011; INPA 3210, 1, 227.9 mm SL, Presidente Figueiredo, Rio Pitinga, downstream from the dam Usina Hidrelétrica de Paranapanema, F. Martinho, 11 October 1989; INPA 10095, 1, 222.3 mm SL, Presidente Figueiredo, Rio Uatumã, Igarapé Arraia, M. Jegú, 15 March 1983; INPA 10092, 1, 206.4 mm SL, Presidente Figueiredo, Rio Uatumã, Usina Hidrelétrica de Balbina, M. Jegú, 01 November 1984; INPA 10090, 3, 223.0–253.9 mm SL, Presidente Figueiredo, Rio Uatumã, cachoeira Miriti, Usina Hidrelétrica de Balbina, M. Jegú, 01 February 1985; INPA 10091, 1, 206.3 mm SL, Presidente Figueiredo, Rio

Uatumã, Igarapé Nazaré, Usina Hidrelétrica de Balbina, M. Jegú, 01 February 1985; INPA 10093, 1, 206.5 mm SL, Presidente Figueiredo, Rio Uatumã, Igarapé Santa Luzia, Usina Hidrelétrica de Balbina, M. Jegú, 01 February 1985; INPA 19972, 1, 163.8 mm SL, Presidente Figueiredo, Rio Uatumã, Usina Hidrelétrica de Balbina, S.A. Amadio, 10 May 1987; INPA 10094, 7, 200.4–258.0 mm SL, Presidente Figueiredo, Rio Uatumã, downstream from the dam Usina Hidrelétrica de Balbina (01°55' S, 59°28' W), J.A. Zuanon, S. Amadio & C. Deus, 01 July 1987; INPA 15577, 1, 160.8 mm SL; INPA 15592, 1, 177.7 mm SL, Presidente Figueiredo, Rio Uatumã, Usina Hidrelétrica de Balbina, S.Amadio, 01 May 1988; INPA 25640, 1, 160.7 mm SL; INPA 25587, 1, 145.7 mm SL; INPA 25641, 1, 194.2 mm SL, Presidente Figueiredo, Rio Uatumã, downstream from the dam Usina Hidrelétrica de Balbina (01°55'12" S, 59°28'19" W), E.G.Ferreira & S.A Amadio, 17 August 2005; INPA 17277, 1, 203.7 mm SL, Amazonas, Santa Luzia, Rio Purus, furo do Lago do Sacado (04°42'48" S, 62°23'54"W), L. Rapp Py-Daniel & C.P. Deus, 03 June 2001; INPA 48834, 1, 191.7 mm SL, Tapauá, Rio Ipixuna, Floresta Tapauá (06°21'17.96" S, 63°14'22.06" W), T. Couto & G.G. Barros, 14 September 2013; INPA 19175, 1, 203.7 mm SL, Tefé, Lago Amanã (02°42'01" S, 64°32'40" W), W.G.R. Crampton, 14 December 1997; MZUSP 67270, 3, 172.7–208.4 mm SL; MZUSP 77623, 1, 210.7 mm SL, Tefé, Rio Tefé, Supiã-Pucu (03°22'00" S 64°43'00" W), M. Goulding, 28 July 1979; INPA 29042, 1, 187.5 mm SL, Carauarí, Rio Juruá, Igarapé Anaxiqui, Reserva de Desenvolvimento Sustentável Uacari, comunidade Boa Vista (05°42'50" S, 67°52'18" W), 25 November 2007; INPA 49177, 1, 201.9 mm SL, Japurá, Rio Japurá, lake on the left bank of the Rio Japurá (01°39'06" S, 69°12'24" W), R. Collins & Marcos, 13 September 2014; INPA 49380, 2, 212.6–231.8 mm SL, Japurá, Rio Japurá, lake on the left bank of the Rio Japurá (01°50'52" S, 69°03'28" W), J. Zuanon, I.M. Soares & P.M. Ito, 30 August 2014. **Mato Grosso:** INPA 10991, 1, 234.5 mm SL, Aripuanã, Rio Aripuanã, Castanhal, Equipe de Ictiologia INPA, 01 August 1976; MZUSP 63019, 1, 129.3 mm SL, São Félix do Araguaia, Rio Araguaia, W. Severi *et al.*, 22 June 1997. **Pará:** INPA 7106, 1, 179.8 mm SL, Aveiro, Rio Cupari, near the confluence with Rio Tapajós (03°44'31" S, 55°23'25" W), L.Rapp Py-Daniel & J.Zuanon, 27 October 1991; MZUSP 67265, 9, 170.0–219.7 mm SL, Belo Monte, Rio Xingu (03°07'00" S, 51°42'00" W), M. Goulding, July–August 1983; MZUSP 106306, 3, 170.6–202.9 mm SL, Rio Xingu, cachoeira Tamaracá (03°07'35" S, 51°41'00" W), Equipe Ictiologia UFPA, 17 December 2000; MZUSP 32412, 2, 202.1–237.0 mm SL, Cuminá, Rio Trombetas

(01°31’00” S, 56° 12’00” W), M. Goulding, October–November 1983; MZUSP 8257, 1, 164.9 mm SL, Oriximiná, Rio Trombetas (01°46’00” S, 55°52’00” W), Expedição Permanente à Amazônia, 16–18 December 1967; INPA 10351, 2, 223.2 to 250.2 mm, Oriximiná, Rio Trombetas, downstream of cachoeira Porteira, E. G. Ferreira & L.Py-Daniel, 03 October 1985; INPA 10352, 2, 153.3–177.9 mm SL, Oriximiná, Rio Trombetas, lago do Tapagem, E. G. Ferreira & L.Py-Daniel, 14 March 1985; INPA 10353, 2, 215.5–217.0 mm SL, same locality and collector as INPA 10352, 14 April 1985; INPA 10354, 1, 156.3 mm SL, Oriximiná, Rio Trombetas, downstream of cachoeira Vira-Mundo, E. G. Ferreira, 08 October 1985; MZUSP 15773, 1, 203.8 mm SL, Rio Trombetas, Igapó do lago Farias, Reserva Biológicas de Trombetas (01°25’00” S, 56°37’00” W), R.M.C. Castro, 15 July 1979; MZUSP 15799, 1, 215.8 mm SL, same locality and collector as MZUSP 15773, 26 July 1979; INPA 16202, 1, 179.9 mm SL, Rio Trombetas, Equipe Ictiologia do INPA, 01 November 1987. MPEG 14872, 3, 211.7–217.6 mm SL, Faro, Rio Nhamundá, Lago do Arco (01°43’22.3” S, 57°11’36.3” W), L.F. Montag, T. Freitas & M. Mendonça, 20 January 2000; MPEG 6579, 1, 225.6 mm SL, Melgaço, Rio Anapu, Baía de Caxiuanã (01°42’8.14” S, 51°22’19.7” W), L.F. Montag, 16 November 2000; MPEG 8690, 1, 249.5 mm SL, Portel, Rio Caxiuanã (01°47’47.4” S, 51°33’12.8” W), L.F. Montag, 20 November 2004; INPA 20553, 1, 211.1 mm SL, Marabá, Rio Tocantins, G.M. Santos, 31 August 2000; INPA 24011, 2, 192.9–202.2 mm SL, Nova Ipixuna, Rio Tocantins, G.M. Santos, 07 October 2004; MPEG 2347, 1, 140.4 mm SL, Porto Jarbas Passarinho, Rio Araguaia, O.R. Cunha, 21 February 1978; INPA 1609, 2, 196.8–203.7 mm SL, Tucuruí, Rio Tocantins, reservatório de Tucuruí, base II (03º56’ S, 49º36’ W), G.M. Santos, 10 November 1981; INPA 1908, 1, 219.8 mm SL, same locality and collector as INPA 1609, 30 September 1984; INPA 1610, 2, 106.6–113.8 mm SL, Tucuruí, Rio Tocantins, upstream of Usina Hidrelétrica de Tucuruí, base IV, G.M. Santos, 05 February 1985; INPA 1608, 1, 190.5 mm SL, Tucuruí, Rio Tocantins, reservatório de Tucuruí, approximately 30 Km of base II (03°34’ S, 49°36’ W), G.M. Santos, 29 March 1985; INPA 2500, 3, 149.2–245.5 mm SL, Tucuruí, Rio Tocantins, F. Martinho, 31 May 1988; INPA 21084, 1, 221.1 mm SL, Rio Tocantins, Jabutizão, G.M. Santos, 06 March 2000; INPA 1607, 1, 108.3 mm SL, Itupiranga, Rio Tocantins (05º 09’ S, 49º 21’ W), G.M. Santos, November 1981. **Rondônia:**15193, 5, 124.7–142.4 mm SL, Candeias do Jamari, Rio Jamari, downstream of Usina Hidrelétrica de Samuel (08°44’16” S, 63°28’26” W), G.M. Santos, 21 June 1988; INPA 10625, 1, 206.8 mm SL, Candeias do Jamari, Rio Candeias, J.P. Viana, 12

August 1993; UFRO-ICT 10844, 2, 194.1–205.7 mm SL, Candeias do Jamari, Rio Candeias, near the mouth of the Rio Jamari (08°37’59” S, 63°33’49.63” W), W.M. Ohara, 14 October 2011; INPA 10621, 1, 205.6 mm SL; INPA 10623, 1, 181.6 mm SL, Rio Jamari, Igarapé Cinco Estrelas (08º44’16” S 63º28’26” W), J.P.Viana, 24 November 1993; INPA 10620, 1, 175.6 mm SL, same locality and collector as INPA 10621, 31 October 1994; INPA 15182, 1, 116.8 mm SL, Porto Velho, Rio Jamari, lago do Rio Verde, approximately 70 Km downstream of Usina Hidrelétrica de Samuel, G.M. Santos, 05 March 1986; INPA 15185, 1, 139.2 mm SL, Porto Velho, Rio Jamari, approximately 15 Km downstream of Usina Hidrelétrica de Samuel, G.M. Santos, 18 June 1988; MZUSP 14033, 1, 206.5 mm SL, Vale do Paraíso, Rio Machado, Lago Paraíso (10°12’00” S, 62°07’00” W), M. Goulding, 14 May 1978. **Roraima:** MPEG 683, 1, 218.4 mm SL, Rio Branco, Igarapé Água Branca, M. Goulding, 09 May 1979; INPA 14044, 1, 194.0 mm SL, Corumbaú, Rio Branco, M. Souza, 27 September 1997. **Tocantins:** NUP 9047, 4, 175.2–193.0 mm SL, Ananás, Rio Araguaia (06°07’24.2” S, 48°18’20.5” W), GERPEL, 11 September 2009; INPA 20204, 1, 208.7 mm SL, Caseara, Rio Araguaia, Lago Casé, E.G. Ferreira, 18 February 2000. **Venezuela:** ANSP 159599, 5 (1 cs), 112.2–128.4 mm SL, Bolivar, Cano (possibly Cano Curimo) feeding río Caura near confluence with río Caura and río Orinoco (07°37’48” N, 64°50’42” W), B.Chernoff, W. Saul & R. Royero, 22 November 1985; ANSP 165819, 5, 110.3–140.2 mm SL, Bolivar, confluence of río Orinoco and río Caura, Las Piedras (07°38’36” N, 64°50’00” W), W. Saul, R. Royero & L. Aguana, 23 November 1985; ANSP 182274, 1, 229.5 mm SL, Amazonas, río Orinoco, bedrock outcrop, 52.9 Km SE of San Antonio and 102 Km W of La Esmeralda (01°06’01” N, 66°27’46” W), M.H. Sabaj, N.K. Lujan, D.C. Werneke & M. Arce, 04 March 2005; AUM 43096, 1, 140.4 mm SL, Amazonas, Pasaganado, río Orinoco, 38 Km N of San Fernando de Atabapo (04°23’3.91” N, 67°46’27.98” W), N.K. Lujan, D.C. Werneke, M.H. Sabaj, M. Arce & T.E. Wesley, 01 March 2005. **Guyana**: AUM 49849, 1, 143.2 mm SL, Region 9 (Upper Takutu), Essequibo, Rupununi river, at Massara landing (03°53’42” N, 59°17’37.32” W), L.S. Souza, D.C Taphorn, J.N. Baskin, T. Geerinckx & J.L. Hwan, 06 November 2007. **Peru:** ANSP 136880, 1, 104.5 mm SL; ANSP 137807, 1, 174.9 mm SL, Loreto, vicinity of Iquitos, Morona Cocha outlet, right bank of Nanay river, ca. 9 mi above Rio Amazonas, C. C.G. Chaplin, M. Hohn, J. Henry & Y. Swabey (Catherwood Peru Expedition), 14 October 1955; MUSM 14402, 1, 105.5 mm SL, Maynas, Loreto, Puerto Almendra, Río Nanay, H. Ortega, 11 December 1986; ANSP 167438, 1, 81.6 mm SL,

Loreto, Río Nanay, right bank 0.5mi below Santa Clara (03°45'00" S, 73°17'00" W), D. Fromm & P. Fromm, 3 September 1990; ANSP 178629, 1, 160.9 mm SL, Maynas, Loreto, Río Nanay, downstream half of large beach (left bank) at village of Pampa Chica, 4.54 Km W of Iquitos, approximaly 11 Km upstream from confluence with Rio Amazonas (03º45'09" S, 73º17'00" W), M.H. Sabaj, M. Littmann, N. Lovejoy, C. Skelton, K. Elkin, M. Thomas & J. Stewart, 2 August 2001; ANSP 182467, 1, 126.3 mm SL, same as locality ANSP 178629, M.H. Sabaj, C. Perez, M. Arce & A. Bullard, 7 August 2005.

***Anostomoides nattereri* (Steindachner, 1876)**

(Figures. 1, 2B, 3B, 4 C and D, 6, 7; Tables 1 and 3)

Leporinus nattereri Steindachner, 1876: 114–117 (type locality: "Mündung des Rio Negro und bei Teffé in den Ausständen des Amazonenstromes…und im Lago Alexo", Brazil). – Garavello & Britski, 2003: 77 (checklist; Essequibo, Orinoco and Solimões rivers).

Anostomoides passionis Santos & Zuanon, 2006: 61–66, fig.; 2 and 3 (diagnosis, description, diagnosis; photos, dentition; ecological notes; type locality: "Rio Xingu, Viracebo do Arroz Cru, State of Pará, Brazil"). – Ohara *et al*., 2017: 34 (brief description, diagnosis in key; Rio Teles Pires). – Sidlauskas & Birindelli, 2017: 85 (cited).

Anostomoides sp. 1. – Santos & Jegú, 1989: 165, fig.; pl. V, fig. 2, 3, 4 and 19 (brief description, diagnosis in key; photo, dentition; lower Rio Tocantins, Brazil).

Diagnosis. *Anostomoides nattereri* differs from *A. atrianalis* by having four branchiostegal rays (*vs.* three), three pores in the infraorbital one (*vs.* four); symphyseal teeth of premaxillary larger, wider, border slightly convex, remaining teeth with truncate border and sometimes with small lateral saliencies forming incipient cusps (*vs.* bicuspid, and remaining teeth slightly tricuspid, with medial cusp distinctly larger, or with blunt cutting edge; lower count of lateral line scales (37–39 *vs.* 41–44); lower jaw lip with dermal papillae (*vs.* lower jaw lip without dermal papillae) (Figure 3); three dark rounded midlateral blotches (*vs.* three or four vertically elongated blotches and/or a faded dark longitudinal stripe), dark lines between scale series on posterior half of body in specimens smaller than 150 mm SL (*vs.* dark lines absent).

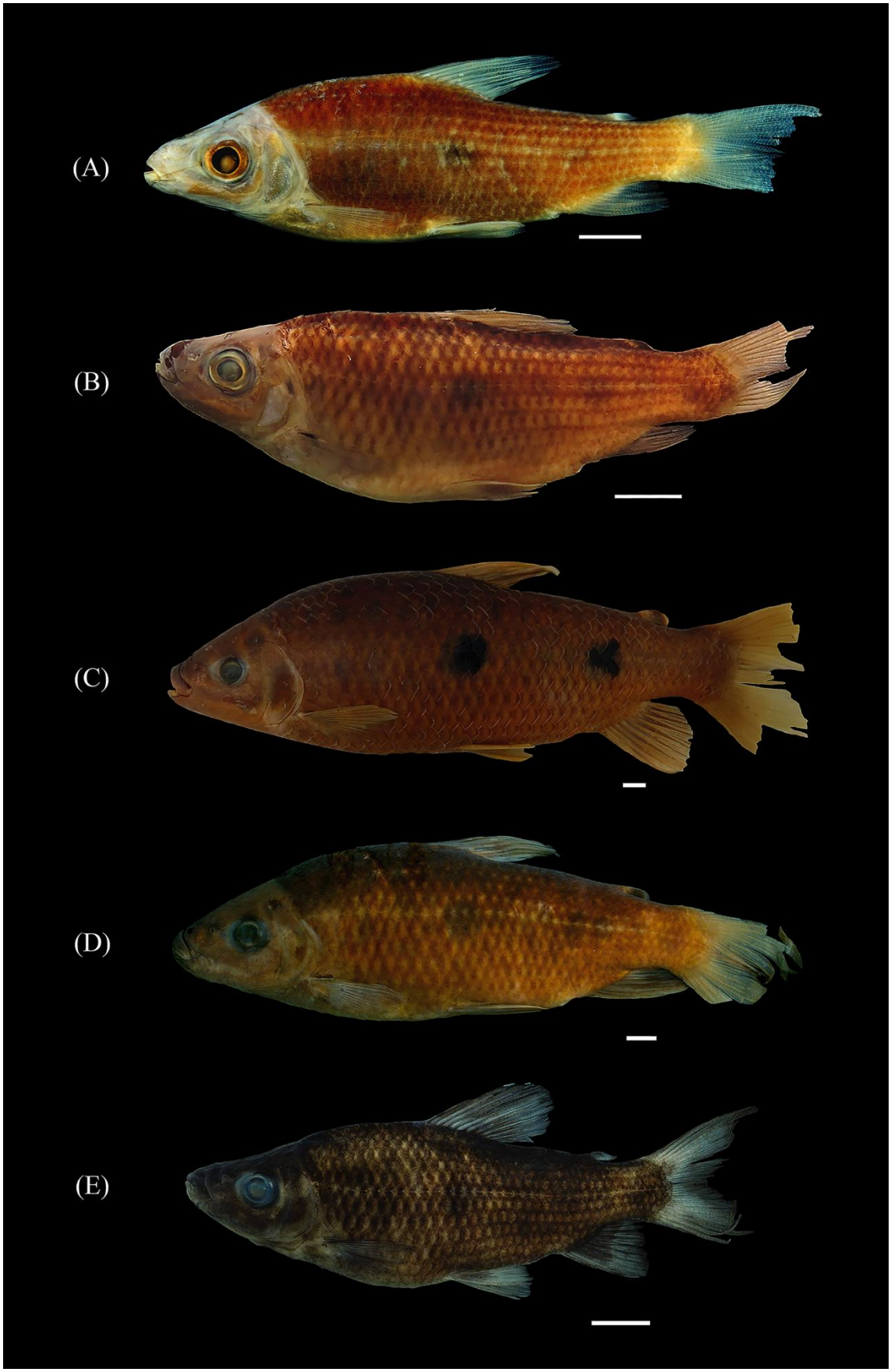


FIGURE 7. *Anostomoides nattereri* from the Amazon basin (A and B) and Rio Xingu (C, D and E): (A) lectotype of *A. nattereri*, NMW 68346, 104.9 mm SL, Brazil,

Amazonas, Rio Tefé; (B) MPEG 19714, 94.2 mm SL, Brazil, Pará, Rio Tapajós; (C) holotype of *A. passionis*, INPA 13182, 265.0 mm SL, Brazil, Pará, Rio Xingu; (D) paratype of *A. passionis*, INPA 14876, 161.0 mm SL, Brazil, Pará, Ponta da ilha da Bela Vista; (E) INPA 47730, 81.3 mm SL, Brazil, Pará, Rio Xingu. Scale bars = 10 mm.

Description. Body elongate, lateraly compressed, greatest body depth at dorsal-fin origin (Table 3). Dorsal profile gently sloped and convex from snout to dorsal-fin base; slightly slanted and convex along dorsal-fin base; somewhat straight or slightly convex from end of dorsal fin to adipose-fin origin, and concave from that point to origin of dorsal procurrent caudal-fin rays (Figure 7). Ventral profile slanted convex from tip lower jaw to vertical through pectoral-fin origin; slightly convex from vertical through pectoral-fin origin to anal-fin origin; slightly convex along anal-fin base, and somewhat concave from anal-fin end to origin of ventral procurrent caudal-fin rays; caudal peduncle sligthly compressed, almost rectangular and slightly longer than deep.

Head pointed in profile and laterally compressed; snout relatively long. Mouth slightly upturned; lips thick and fleshy, covered internally with numerous papillae. Four premaxillary teeth, symphyseal teeth larger, wider, border slightly convex, remaining teeth with truncate border and sometimes with small lateral saliencies forming incipient cusps. Four dentary teeth gently decreasing in size laterally, two medial teeth with truncate cutting edge without cusps, and two lateral teeth with three to five small cusps. Lower jaw lips fringed and covered with conical or hemi-cylindrical dermal papillae. Four branchiostegal rays.

Scales large and cycloid. Lateral line complete with 37(3)*, 38(48) or 39(1) perforated scales, extending from supracleithrum to basis of middle caudal-fin rays. Horizontal scale rows between dorsal-fin origin and lateral line 5(2), 6(32) or 7(9). Horizontal scale rows between lateral line and pelvic-fin origin 5(27) or 6(15). Horizontal scale rows around caudal peduncle 16(51)*. Predorsal scales from dorsal-fin origin to tip of supraoccipital spine 12(10), 13(11), 14(7), 15(8) or 16 (6).

Dorsal-fin rays ii, 9(3), ii, 10(39), ii, 11(9)* or iii, 11(1). Dorsal-fin origin slightly anterior to middle of standard length; distal margin of dorsal fin straight or gently concave. Adipose fin small, slightly rectangular shaped, its origin approximately at vertical through half of anal-fin base length. Pectoral-fin rays i, 12(1), 14(34)* or 15(17); its tip extending more than half distance between origins of pectoral and pelvic fins; pectoral fin base slightly convex; its distal margin slightly convex. Pelvic-fin rays

i, 8(51)*; with distal margin slightly convex. Anal-fin rays ii, 8(4), iii, 8(37), ii, 9(5)* or iii, 9(5); its origin approximately at vertical through fifth scale anterior to adipose-fin origin; distal margin of anal fin straight or gently concave. Principal caudal-fin rays i, 9+8,i (51)*. Caudal fin forked, upper lobe slightly longer than lower lobe.

TABLE 3. Morphometrics of *Anostomoides nattereri.* N = Number of specimens, N = Number of specimens, Min = Minimum, Max = maximum, Mean = average, SD = standard deviation.

Character	Lectotype	N	Min – Max	Mean	SD
Standard length (mm)	104.9	42	78.1–268.4	174.7	56.5
Percents of standard length					
Adipose-fin origin to hypural joint	15.3	42	11.9–20.6	17.1	1.3
Body depth	31.5	42	24.5–38.7	30.0	2.3
Body width	–	42	9.4–17.4	11.7	1.0
Caudal-peduncle depth	11.2	42	9.3–13.6	10.9	0.6
Caudal-peduncle length	11.6	42	11.4–17.1	14.2	1.1
Dorsal-fin origin to adipose-fin origin	38.9	42	37.2–52.1	42.1	2.1
Dorsal-fin origin to caudal-fin origin	43.2	42	41.2–70.8	57.7	3.4
Head length	28.4	42	19.7–30.3	23.4	1.7
Lower jaw to adiposa-fin origin	71.2	42	79.0–104.9	84.0	2.5
Lower jaw to anal-fin origin	66.4	42	74.6–98.4	78.4	2.2
Lower jaw to dorsal-fin origin	48.4	42	38.9–57.1	43.9	2.3
Lower jaw to pectoral-fin origin	23.1	42	18.0–29.4	22.7	1.9
Lower jaw to pelvic-fin origin	53.05	42	42.9–61.5	47.4	2.1
Percents of head length					
Bony interorbital	37.4	42	42.6–67.3	53.9	3.9
Eye diameter	28.4	42	22.0–39.5	29.4	2.4
Head depth	77.5	42	80.1–132.9	104.9	10.9
Preopercle depth	53.4	42	66.8–119.8	87.2	9.2
Preopercle length	77.6	42	64.0–100.6	73.7	4.4
Snout depth	106.12	42	34.4–90.4	56.3	6.8
Snout length	38.9	42	25.0–44.1	34.3	3.3

Coloration in alcohol. Body with background color light brown to beige (Figure 7). Body with three inconspicuous midlateral rounded dark brown blotches in small specimens (up to 200 mm SL): first one below dorsal-fin base; second blotch above anal-fin origin; third blotch at caudal peduncle terminus. Body with two conspicuous round dark midlateral in large specimens (from 200 mm SL): first blotch below dorsal-fin base; second above anal-fin origin. Dark midlateral blotches covered by epidermal dark pigmentation in large specimens (more than 200 mm SL), blotches circle-shaped. Posterior portion of body (from vertical through dorsal-fin origin to terminus of caudal peduncle) with dark lines between scale series in specimens smaller than 150 mm SL. Dorsal fin with rays and interradial membranes pale on proximal portion and dark on median and distal areas, or uniformely tan. Caudal, pectoral and pelvic fins uniformly tan. Anal fin with rays and interradial membranes pale on proximal area and dark on median and distal area. Adipose fin with base and lobe pale, except median portion, which is light dark.

Distribution. *Anostomoides nattereri* is distributed in the Amazon river and in the following tributaries at the Amazon basin: Negro, Tefé, Tapajós, Tocantins and Xingu river basins Brazil (Figure 8).

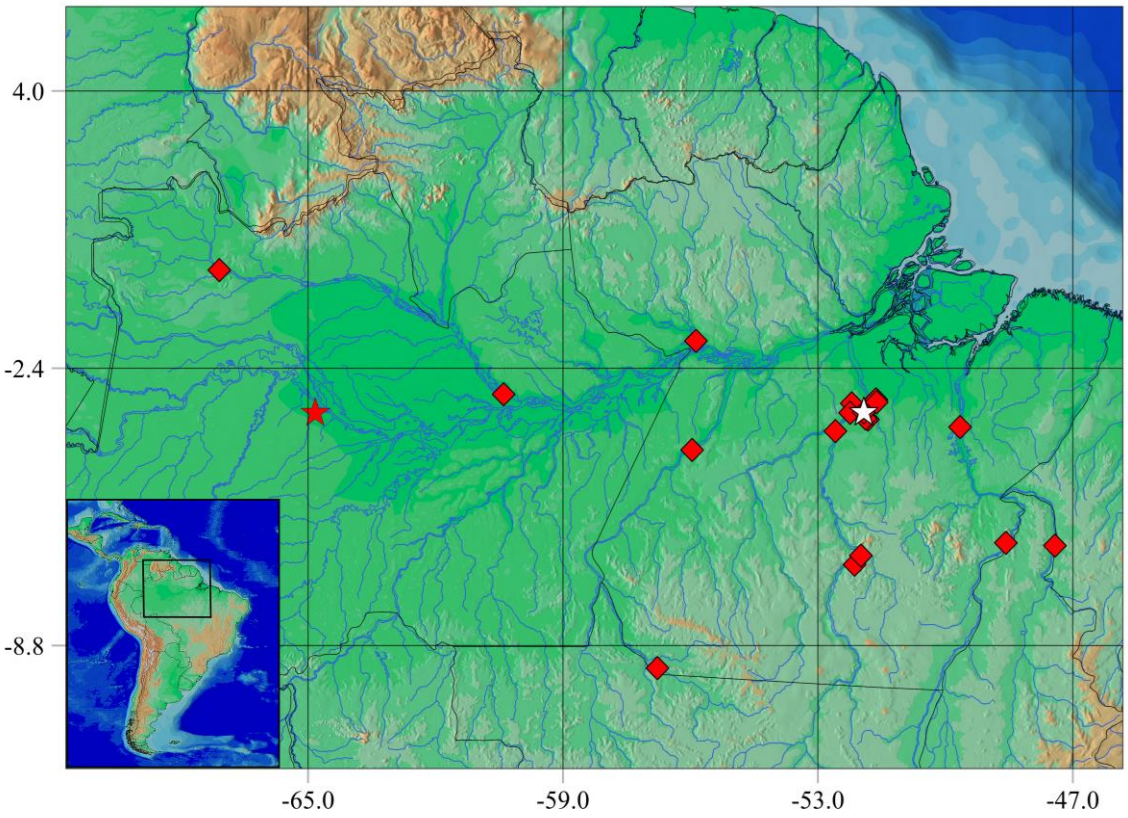


FIGURE 8. Geographic distribution of species of *Anostomoides nattereri:* red star: type locality of *A. nattereri*; white star: type locality of *A. passionis*; and red diamond: records of *A. nattereri.* Some symbols may correspond to more than one locality.

Common names. The presence of a large head is usually associated in the Brazilian fish literature with the common names "aracu cabeça gorda" (Santos *et al*., 1984; Santos *et al*., 2006) or "piau de cabeça gorda" (Santos *et al*., 1984; Ferreira *et al*., 1998; Santos *et al*., 2006). On the other hand, *Anostomoides nattereri* is popularly called as "aracu vermelho" (Santos, 2004) or "piau do sarão" (Santos & Zuanon, 2006).

Remarks. Steindachner (1876) described *Leporinus nattereri* based on several specimens from the Amazon basin. The name *Leporinus nattereri* is occasionally cited in regional checklists (*e.g.*, Lasso *et al*., 2004; Ocampo *et al.*, 2008; Sarmiento *et a*l., 2014), but it cannot be assumed that these citations truly refer to specimens conspecific with the species described by Steindachner (1876).

All 12 syntypes of *Anostomoides nattereri* deposited in the MCZ and in the NMW were examined. Even though the type specimens of *A. nattereri* include several individuals collected in distinct sites, they are in fact all conspecific. One specimen from Tefé (NMW 68346) relatively large (104.9 mm SL) and well-preserved is herein selected as lectotype.

Anostomoides nattereri was reported in Bolivia and Colombia (Lasso *et al*., 2004; Ocampo *et al*., 2008; Sarmiento *et al*., 2014). Even though we were not able to examine specimens collected outside Brazil, the wide distribution of *A. nattereri* indicates that it is likely that the species occurs in other South-American countries.

Material Examined. Type material: NMW 68346, 1, 104.9 mm SL, Brazil, Amazonas, Rio Tefé, J. Natterer, Austrian Expedition in Brazil (1817–1835), lectotype of *Anostomoides nattereri*, by present designation. MCZ 20384, 3, 79.0–103.0 mm SL, Brazil, Amazonas, confluence between the Rio Tefé and Rio Solimões (03°24' S, 64°45' W), L. Agassiz, Thayer Expedition, October 1865; NMW 68344, 3, 79.9–86.9 mm SL, Brazil, Amazonas, Lago Aleixo, F. Steindachner, 1874; NMW 68345, 4, 67.2–81.3 mm SL, same as NMW 68344; NMW 68346b, 1, 101.2 mm SL, same as NMW 68346. INPA 13182, 1, 265.0 mm SL, Brazil, Pará, Rio Xingu, Viracebo do Arroz Cru (03°25'15" S, 51°55'08" W); G.M. Santos & J. Zuanon, 17 September 1997. Holotype of *Anostomoides passionis*. INPA 4043, 2, 229.6–268.2 mm SL, same as INPA 13182;

MZUSP 86023, 1, 268.4 mm SL same as INPA 13182. Paratypes of *Anostomoides passionis.*

Non types. Brazil: Amazonas: INPA 14042, 1, 88.5 mm SL, Manaus, Rio Branco, C.C. Fernandes, 15 November 1992; MZUSP 14452, 1, 193.3 mm SL, Manaus, Rio Negro, Igarapé Jaraqui (03°00’ S, 60°24’ W), Expedição Permanente à Amazônia, April 1967; INPA 14043, 1, 89.0 mm SL, Manaus, Rio Negro, right side, near the confluence with Rio Branco, M.Souza, 28 September 1997; NMW 87756, 1, 163.0 mm SL, Tefé, mouth Rio Negro; MZUSP 77615, 1, 170.3 mm SL, São Gabriel da Cachoeira, Rio Negro, Igapó (00°07’ S, 67°05’ W), M. Goulding, 18 May 1979. **Maranhão:** UNT 83, 2, 215.0–236.3.mm SL, Estreito, Rio Tocantins, near the confluence with the Rio Itaueira (06°30’ S, 47°25’ W), NEAMB – UFT, 29 June 2000; MNRJ 39644, 1, 213.0 mm SL, Estreito, Rio Tocantins, drained stretch for the construction of the Usina Hidrelétrica de Estreito, D.F. Morais, E. Dubanskas & M. Senna, 06 March 2010. **Mato Grosso:** INPA 45078, 1, 162.1 mm SL, Paranaíta, Rio Teles Pires, downstream of Sete Quedas, Solange, Reginaldo & Rosalvo, February 2014; MZUSP 54551, 1, 163.2 mm SL, São Francisco do Araguaia, Rio Araguaia Coleção Rio Araguaia, February 1998. **Pará:** MZUSP 110595, 2 (Sk), 230.0–232.0 mm SL, Altamira, Rio Bacajai (03° 52' 11" S, 51° 52' 48.0" W), O.T. Oyakawa, J.L.O. Birindelli, C. Moreira, A. Akama, L. Sousa & H. Varella, 19 November 2000; MZUSP 105643, 1, 239.6 mm SL, Altamira, Rio Xingu, Caitucá (03° 33' 44" S, 51° 52' 37" W, Equipe de Ictiologia da UFPA, 05 – 06 November 2000; INPA 47730, 1, 81.3 mm SL, Altamira, Rio Xingu, approximately 4 km above the confluence with the Rio Iriri (03°51’08” S, 52°35’17” W), M. Sabaj, 02 November 2014; INPA 47181, 1, 256.3 mm SL, Altamira, Rio Xingu, beach at 59 km from Altamira (03°35’01” S, 51°49’23” W), M. Sabaj, 10 November 2014; INPA 40489, 1, 88.8 mm SL, Anapu, Rio Xingu, below of the Volta Grande, near Cachoeira Camaraca (03°07'13" S, 51°38'01" W), M. Sabaj, 21 September 2013; INPA 40753, 5, 78.1–176.0 mm SL, Anapu, Rio Xingu, below of the Volta Grande (03°11'03" S, 51°37'02" W), M. Sabaj, 28 September 2013; INPA 40840, 1, 264.4 mm SL, Anapu, Rio Xingu, below of the Volta Grande and Cachoeira Tamaracá (03°07'41" S, 51°37'17" W), M. Sabaj, 01 October 2013; MPEG 19714, 1, 94.2 mm SL, Itaituba, Rio Tapajós, vila de Miriticuba (04°17'13.8" S, 55°57'36.2" W), C.S. Ramos, 09 July 2010; INPA 1613, 2, 95.1–155.2 mm SL, same locality and collector as INPA 1607, 01 September 1980; INPA 24014, 1, 207.2 mm SL, Nova Ipixuna, Rio Tocantins, reservoir of

Hidrelétrica de Tucuruí, G.M. Santos, 07 October 2004; MZUSP 5429, 6 (1 Sk), 131.9–169.5 mm SL, Oriximiná, Rio Trombetas (01°46’ S, 55°52’ W), Expedição Permanente à Amazônia, February – March 1967; INPA 53134, 1, 186.3 mm SL, Tucuruí, Rio Tocantins, reservoir of Hidrelétrica Tucuruí, base II (03º56’ S, 49º36’ W), G.M. Santos, September 1984; INPA 2501, 1, 195.2 mm SL, Tucuruí, Rio Tocantins, F. Martinho, 31 May 1988; INPA 20565, 1, 232.0 mm SL, Tucuruí, Rio Tocantins, downstream from the dam Usina Hidrelétrica de Tucuruí (03°45'30" S, 49°39'10" W), Equipe Eletronorte, 16 May 2000; INPA 24013, 2, 207.2–216.2 mm SL, same locality as INPA 20565, G.M. Santos, 27 October 2004; LIA 1229, 1, 175.5 mm SL, São Félix do Xingu, Rio Pedra Preta (06°43'29.35" S, 51°58'54.12" W), L. Souza, A. Gonçalves & C. Martins, 22 September 2014; LIA 1157, 1, 104.6 mm SL, São Félix do Xingu, Rio Remansinho (06°55'58.48"S, 52°08'13.45" W), L. Souza, A. Gonçalves & C. Martins, 23 September 2014. **Tocantins:** NUP 8383, 1, 177.8 mm SL, Tocantins, Xambioá, Rio Araguaia (06°25'49" S, 48°34'32" W), GERPEL, 23 March 2009.

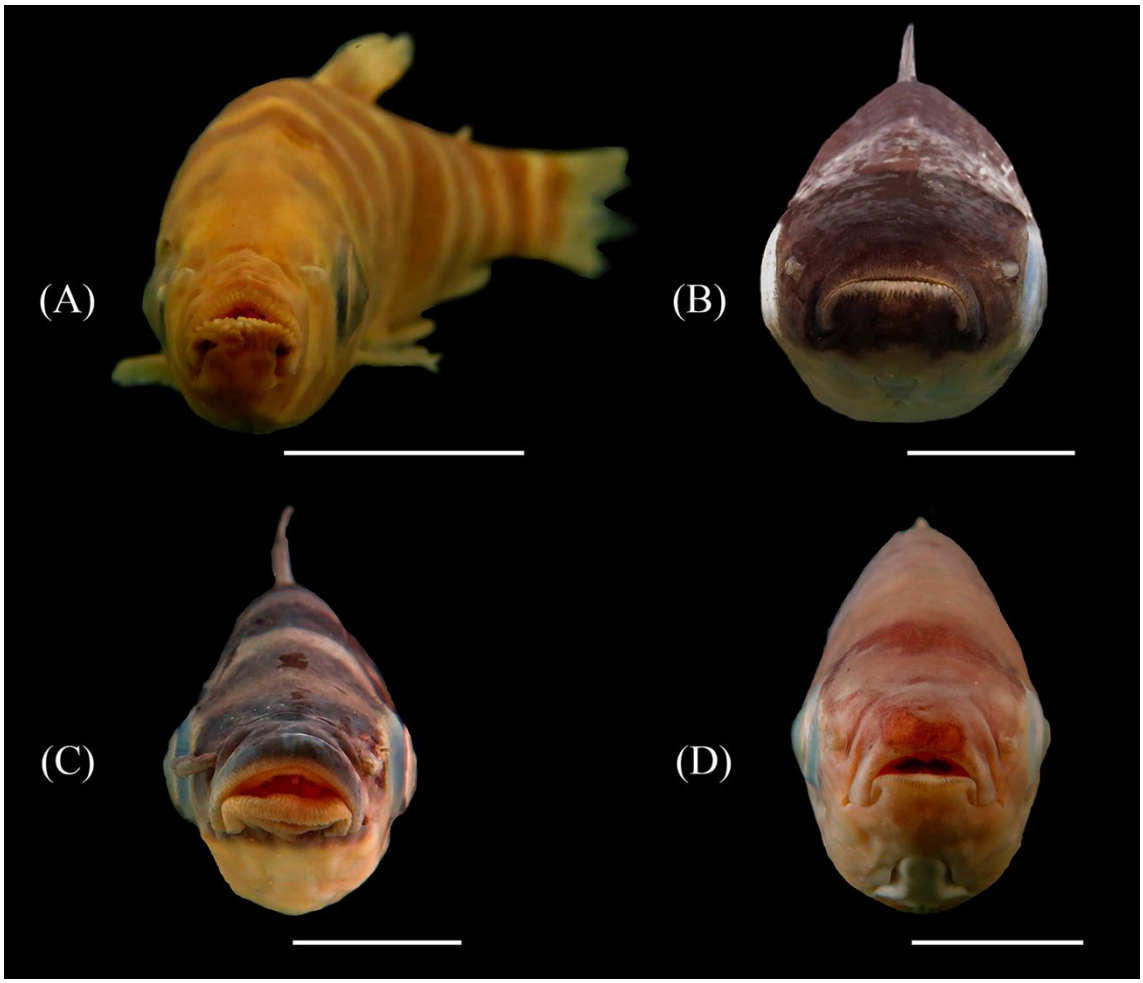


FIGURE 9. Frontal view of the head showing thickened, fringed lips with numerous dermal papillae in: (A) *Synaptolaemus latofaciatus*, MZUEL 14112, 72.0 mm SL; (B)

thickened, fringed lips in *Laemolyta taeniata*, MZUEL 14859, 149.5 mm SL and (C) *Leporinus fasciatus*, MZUEL 14698, 136.3 mm SL; (D) thickened lips without fringes in *Leporinus friderici*, MZUEL 4986, 126.2 mm SL. Scale bar = 10 mm.

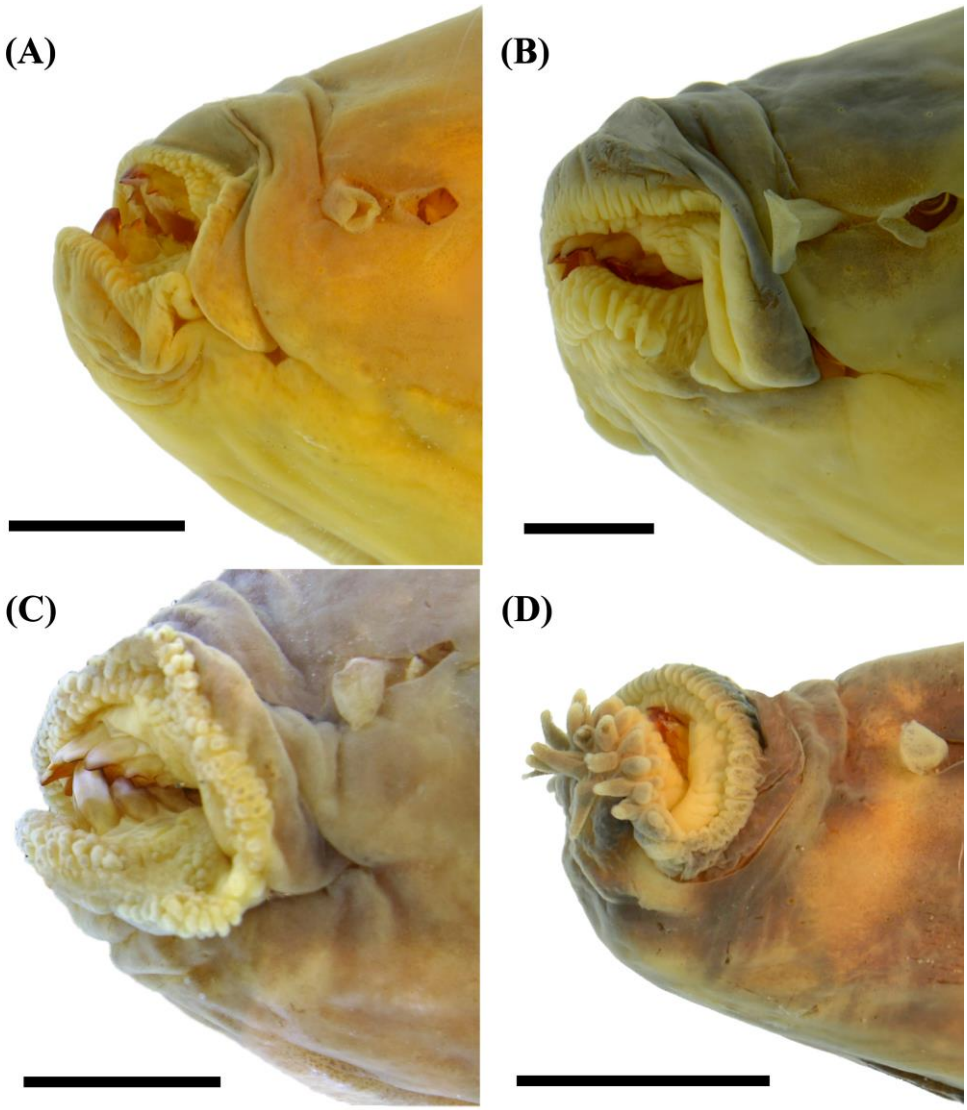


FIGURE 10 Lateral view of the head showing thickened, fringed lips with numerous dermal papillae in: (A) *Anostomoides atrianalis*, ANSP 159599, 132.8 mm SL, (B) *Leporinus fasciatus*, ANSP 161713, 189.9 mm SL, (C) *Anostomoides nattereri*, FMNH 103451, 141.8 mm SL, (D) *Synaptolaemus latofasciatus*, ANSP 190764, 80.2 mm SL. Scale bar = 5 mm.

Discussion

The extensive analyses of meristic data as well as color pattern conducted here showed that the four nominal species of *Anostomoides* represent two valid species based on discrete differences in both counts and measurements of individuals (see Diagnoses). In addition, the Principal Components Analysis (PCA) (Figure 1) discriminated two groups, the first comprising specimens of *A. atrianalis* from the Amazon, Essequibo and Orinoco river basins, and the second formed by specimens of *A. nattereri* from the Amazon, Tapajós, Tocantins and Xingu basins. Specimens of *A. atrianalis* are easily distinguished from *A. nattereri* based on meristic data and color pattern. In addition, *A. atrianalis* shows greater interorbital distance (42.6–67.3 % *vs.* 34.4–53.8 % of HL) (Fig. 3).

Specimens of *Anostomoides nattereri* are also easily distinguished from *A. atrianalis* by presenting lower jaw lip covered with conical or hemi-cylindrical dermal papillae (*vs.* lip fleshy, thick and fringed) (Fig. 4). The lower jaw lip in *A. atrianalis* is similar to that described by Birindelli *et al*. (2012) for *Pseudanos varii* in which the lower jaw lips are fleshy and fringed. When analyzing other species of anostomids, we observed that the lower jaw lip is always fleshy and with distinct degrees of fringing as illustrated in Fig. 8. Winterbottom (1980) and Sidlauskas & Vari (2008) noted that only the genera *Gnathodolus*, *Sartor* and *Synaptolaemus* possesses the lower jaw lip with dermal papillae. Santos & Zuanon (2006) also noted the fringed flesh lip when describing *Anostomoides passionis*.

Géry (1977) and Santos & Zuanon (2006) distinguished *A. atrianalis* from *A. laticeps* in a key to species identification based on the plain color of the body and anal fin with 10 branched rays in the former (*vs*. three transverse bands plus dark pigmentation at caudal base and eight branched anal-fin rays in the latter). However, the types, and specimens collected in localities close to the type locality of *A. atrianalis*, exhibit eigth branched rays in the anal fin, and possess three or four vertically elongated blotches and/or a faded dark longitudinal stripe.

Géry (1977) based his diagnosis of *A. atrianalis* on the description presented by Pellegrin (1909), who included branched and unbranched rays in the count of anal-fin rays, and on the faded coloration exihibited by the types of *A. atrianalis*. Santos & Zuanon (2006) followed the information provided by Géry (1977). Santos & Zuanon (2006) *A. atrianalis* a specimen rare in collections and also in nature. Sidlauskas & Vari (2012), in their inventory of the fishes of Guyana, did not have samples of

Anostomoides, despite having specimens of other species collected in the type locality of *A. laticeps* (Crab Falls, Essequibo river drainage). We were able to examine a single non-type specimen collected in the Guyana (AUM 49849), confirming the hypothesis of synonym between *A. atrianalis* and *A. laticeps*.

Anostomoides nattereri is widely distributed in the Amazon basin, including the Negro, Tapajós, Tocantins and Xingu basins, and possibly rivers in Bolivia and Colombia. Nevertheless, it is a species poorly documented, possibly, due to misidentification (*e.g.*, Santos & Jégu, 1989). Garavello (1979), in his revision of *Leporinus*, based *A. nattereri* diagnosis on only ten specimens from a few localities (including Rio Negro and Rio Tefé), what may have contributed to subsequent misidentified (*e.g.*, Santos & Jégu, 1989), and the recent description of *Anostomoides passionis*, a junior synonym.

The genus *Anostomoides* is distinguished among Anostomidae by having a combination of non-exclusive features. *Anostomoides atrianalis* has an upturned mouth and *A. nattereri* has a slightly upturned mouth (Figure 2). Among Anostomidae, an upturned mouth is present in *Laemolyta*, and in the Anostominae (*Anostomus*, *Gnathodolus, Petulanos*, *Pseudanos*, *Sartor* and *Synaptolaemus*). On the other hand, other genera of the Anostomidae possess a terminal mouth, such as *Abramites*, *Schizodon*, *Rhytiodus* and some species of *Leporinus*; or downturned mouth, as *Hypomasticus*, *Leporellus, Megaleporinus* and some species of *Leporinus*. Winterbottom (1980) considered an upturned mouth ("supraterminal" in his terminology) present only in Anostominae. *Laemolyta* and *Anostomoides* were considered by previous authors (Géry, 1977; Winterbottom, 1980; Mautari & Menezes, 2006) as presenting an intermediate condition between a terminal mouth (as in some *Leporinus*, for example) and the upturned mouth of Anostominae. Even though this interpretation is corroborated herein for *A. atrianalis*, it is not entirely true for *A. nattereri*, which have a slightly less upturned mouth. This help to show that the mouth position varies continuously among species of Anostomidae, as, there is also a great variation in this feature in the remaining anostomids, in which mouth vary continually from terminal to downturned. In fact, this variation can be seen in distinct ontogenetic stages of a single species (*e.g.*, Birindelli & Britski, 2009; Machado-Evangelista *et al.*, 2015). Recent phylogenetic analyses based on molecular data show that the mouth position has changed independently in some groups of Anostomidae (Ramirez *et al.*, 2016, 2017).

The Anostomidae presents a wide variation in the shape and number of premaxilla and dentary teeth among species and especially among genera. Despite this variation, some clearly distinguishable patterns exist and teeth morphology is used, at least since Myers (1950), as a rich source of diagnostic features to define genera of Anostomidae. In fact, a few species are diagnosed almost exclusively based on teeth morphology (*e.g.*, *Leporinus geminis* Garavello & Santos, 2009) and number (*e.g.*, *Leporinus venerei* Britski & Birindelli, 2008). The number of teeth on each premaxilla and dentary in most anostomids is four, as it is in both species of *Anostomoides*. However, reduction of the number of teeth occurs in several species, including *Abramites*, *Sartor* and in some species of *Leporinus*, *Megaleporinus* and *Hypomasticus* (Britski & Birindelli, 2008; Ramirez *et al*., 2017). The extreme condition of a single tooth in dentary is present in *Gnathodolus* (Myers, 1927). Sidlauskas & Vari (2008) considered a continuously rounded tooth with no distinct point of inflection as a unicuspid tooth. According to this definition all members of the family have at least one cusp on their teeth. However, adult specimens of several genera as *Anostomus*, *Pseudanos*, *Petulanos*, *Schizodon*, and *Rhytiodus* have three of four distinct cusps of similar size on the premaxillary and dentary teeth (Myers, 1950; Winterbottom, 1980; Sidlauskas & Vari, 2008; Ramirez *et al*., 2016), or only on the premaxillary teeth as in *Laemolyta* (Mautari & Menezes, 2006). On the other hand, adult specimens of *Hypomasticus*, *Megaleporinus*, *Leporellus* and *Leporinus* have generally unicuspid teeth (rarely bicuspid) on the premaxillary and dentary bones (Birindelli & Britski, 2013; Birindelli *et al*., 2013, Birindelli & Teixeira, 2016; Ramirez *et al*., 2016). Juvenile specimens of these four genera have teeth with three cusps (rarely four or five cusps) with median cusps distinctly larger (Sidlauskas & Vari, 2008), showing that teeth morphology also changes ontogenetically. Unique conditions of teeth morphology are present in *Abramites*, which possesses the first two teeth of the dentary bone with two cusps and remaining teeth unicuspid (Vari & Williams, 1987; Sidlauskas & Vari, 2008), and in *Sartor* and *Gnathodolus*, that possess an enlarged sickle-shaped symphyseal tooth on the dentary bone and remaining teeth absent or reduced in size and cusp number (Myers, 1927; Winterbottom, 1980; Sidlauskas & Vari, 2008). Adult specimens of *Anostomoides* possess teeth morphology similar to the species of *Hypomasticus*, *Megaleporinus*, *Leporellus*, and *Leporinus*, in which the premaxillary and dentary bones possess unicuspid or bicuspid symphyseal teeth (forming a blunt cutting edge) and remaining teeth with small cusps (three or even more cusps in some specimens). So,

even though the teeth morphology of *Anostomoides* is not exclusive, it helps to distinguish the genus from most other genera of Anostomidae.

The monophyly of *Anostomoides* is currently not supported by any exclusive features and must be tested in a phylegenetic framework, something beyond the scope of the present contribution.

Comparative material examined. All from Brazil, except if otherwise noted.
Abramites hypselonotus: Acre: MZUEL 5425, 3, 74.4–110.3 mm SL, Rio Branco, Rio Acre, Praia D. Bela, O.A. Shibatta, 28 August 2009; Mato Grosso do Sul: MZUEL 13599, 2, 96.1–97.5 mm SL, Corumbá, Estrada Parque, Vazante 38, Drenagem do Rio Paraguai (19°32'28.49" S, 57°02'23.2" W), O.A. Shibatta, 18 August 2008. *Anostomus ternetzi*: Mato Grosso: MZUEL 7629, 2, 53.9–65.9 mm SL, Barra do Garça, Rio Corrente (15°29'56.9" S, 52° 42' 40.5" W), L.R. Jarduli, W.B. Ruiz & E. Santana, 31 July 2008. *Gnathodolus bidens*: Rondônia: MZUEL 14113, 1, 58.3 mm SL, Candeias do Jamari, Rio Jamari, Canal de desvio da Usina Hidrelétrica de Samuel, G.M. Santos, 07 June 1988; *Laemolyta proxima*: Amazonas: MZUEL 17132, 1, 216.2 mm SL, Manaus, Doação INPA, sem dados, O.A. Shibatta, 03 July 2003. *Laemolyta taeniata*: Amazonas: MZUEL 14859, 5, 149.5–200.7 mm SL, Novo Airão, Rio Negro, Praia do Saraá, Parque Nacional de Anavilhanas (02°36'49.46" S, 60°57'19.55" W), J.L.O. Birindelli, F. Jerep, L. Rapp Py-Daniel, D. Bastos, R. Ota, & S. Hashimoto, 06 May 2016. *Leporellus vittatus*: Minas Gerais: MZUEL 16409, 1, 139.3 mm SL, Buritizeiro, Rio São Francisco (17°12'56.9" S, 44°56'07.8" W), J.L.O. Birindelli, F.C. Jerep, E. Santana & R.H.C. Nascimento, 07 July 2016; Paraná, MZUEL 4694, 1, 148.6 mm SL, Londrina, Rio Taquara, Distrito de Maravilha (23°30'51" S, 50°57'18" W), W. Galves, 13 December 2006. *Leporinus fasciatus*: Amazonas: MZUEL 14698, 3, 136.3–203.3 mm SL, Novo Airão, Rio Negro, Lago do Prato, Parque Nacional de Anavilhanas (02°43'2.50" S, 60°44'41.53" W) J.L.O. Birindelli, F. Jerep, L. Rapp Py-Daniel, D. Bastos, R. Ota, & S. Hashimoto, 03 May 2016; *Leporinus friderici*: Paraná: MZUEL 4986, 1, 126.2 mm SL, Paraná, Londrina, ribeirão Três Bocas, Parque Ecológico Dr. Daisaku Ikeda (23° 23' 06" S, 51°04'33" W), L.G. Caetano, 03 December 2007; MZUEL 384, 2, 104.9–115.6 mm SL, Paraná, Sapopema, Rio Tibagi, Porto do Areia (24°01'26" S, 50°41'51" W), ECPUEL, 05 May 1990. *Leporinus piau*: Maranhão: MZUEL 17418, 2, 138.1–141.75 mm SL, Rio Turiaçu (02°15'49" S, 45°19'24" W), E.C. Fraga, W.M.M. Pires & R.C Lima, 03 July 2015; *Leporinus steindachneri*: MZUEL

16474, 6, 100.4–207.1 mm SL, Minas Gerais, Águas Vermelhas, Rio Pardo downstream of Usina Hidrelétrica de Machado Mineiro (15°31'16.3" S, 41°30'14.8" W), J.L.O. Birindelli, F.C. Jerep, E. Santana & R.H.C. Nascimento, 03 July 2016. *Megaleporinus piavussu*: MZUEL 4245, 1, 96.6 mm SL, Paraná, Jataizinho, ribeirão Taquari (23°12'24" S, 50°55'50" W), ECPUEL, 22 October 1999. *Megaleporinus obtusidens*: MZUEL 18367,1, 151.8 mm SL, Rio Grande do Sul, Itaqui, Rio Uruguai, approximately Rio Ibicuí (29°06'59.2" S, 56°33'47.8" W), LAPAD–UFSC, 24 November 2016. *Megaleporinus reinhardti*: MZUEL 7058, 1, 120.3 mm SL, Bahia, Bom Jesus da Lapa, Rio São Francisco, upstream Bom Jesus da Lapa (13°19'12" S, 43°27'30" W), A. Akama & J.L.O. Birindelli, 16 February 2011. *Pseudanos varii*: MZUEL 14695, 5, 80.1–118.6 mm SL, Amazonas, Novo Airão, Rio Negro, Lago do Prato, Parque Nacional de Anavilhanas (02°43'2.50" S, 60°44'41.53" W), J.L.O. Birindelli, F. Jerep, L. Rapp Py-Daniel, D. Bastos, R. Ota, & S. Hashimoto, 03 May 2016; *Rhythiodus microlepis*: MZUEL 17133, 1, 238.9 mm SL, Amazonas, Manaus, Doação INPA, sem dados, O.A. Shibatta, 03 July 2003. *Synaptolaemus latofasciatus*: Amazonas: MZUEL 14112, 1, 72.0 mm SL, Presidente Figueiredo, Rio Uatumã, cachoeira do Miriti (01°40' S, 59°39' W), E. G. Ferreira, R.G. Leite & S. Kullander, 04 October 1987.

Acknowledgments

We are grateful to O. Shibatta and F. Jerep (UEL), B. Sidlauskas (OSU), C. Moreira (UFRJ), J.C. Garavello (UFSCAR). G.C. Silva (UNESP-Botucatu), F.O. Martins (IFPR-Londrina), J. Zuanon (INPA) and F.C.T. Lima (ZUEC) for discussions and valuable suggestions to the present study. For loans and exchange of specimens we thank: A. Datovo (MZUSP), C.S. Pavanelli (NUPÉLIA-UEM), H. Ortega (MUSM), L. Rapp Py-Daniel (INPA), L. Sousa (LIA-UFPA), M.R.M. Fernandes (UFRO-ICT), M. Sabaj (ANSP), J. Armbruster and D. Werneke (AUM), M.R. Britto (MNRJ), and W.B. Wosiacki (MPEG). We thank A. Datovo, M.D. Gianeti and O. Oyakawa (MZUSP), and L. Rapp Py-Daniel (INPA) for the assistance during visits to their respective collections and to D. Le, K. Swagel and C. McMahan (FMNH) for a picture of the holotype of *A. laticeps*. The first author thanks Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) by financial support.

References

Bemis, W.E., Hilton, E.J., Brown, B., Arrindell, R., Richmond, A.M., Little, C.D., Grande, L., Forey, P.L. & Nelson, G.J. (2004) Methods for preparing dry, partially articulated skeletons of Osteichthyans, with notes on making Ridewood dissections of the cranial skeleton. *Copeia*, 3, 603–609.

Bertin, L., & Dolfuss, R. P. (1948) Révision des espèces du genre Decapterus (Téleostéens Scombriformes). *Mémoires du Muséum National d'Histoire Naturelle*, 26(1), 1–29.

Birindelli, J.L.O. & Britski, H.A. (2009) New species of *Leporinus* Agassiz (Characiformes: Anostomidae) from the Rio Curuá, Rio Xingu basin, Serra do Cachimbo, Brazil, with comments on *Leporinus reticulatus*. *Neotropical Ichthyology,* 7(1), 1–10.

Birindelli, J.L.O., Lima, F.C.T & Britski, H.A**.** (2012) New species of *Pseudanos* Winterbottom, 1980 (Characiformes: Anostomidae) with notes on the taxonomy of *P. gracilis* and *P. trimaculatus*. *Zootaxa,* 3425, 55–68.

Birindelli, J.L.O. & Britski, H.A**.** (2013) Two new species of (Characiformes: Anostomidae) from the Brazilian Amazon, and redescription of Kner 1858. *Journal of Fish Biology,* 83(5), 1128–1160.

Birindelli, J.L.O., Britski, H.A**.** & Garavello, J.C. (2013) Two new species of *Leporinus* Agassiz (Characiformes: Anostomidae) from eastern basins of Brazil, and redescription of L. melanopleura Günther. *Neotropical Ichthyology,* 11(1), 9–23.

Birindelli, J.L.O. & Teixeira, T.F. (2016) Two new species of *Leporinus* Agassiz, 1929 (Characiformes: Anostomidae) from tributaries of the lower Amazon basin in Brazil. *Zootaxa*, 4178 (1), 97-115.

Borodin, N.A. (1931) On the genus *Anostomus* (Family Characinidae). *Bulletin of the Museum of Comparative Zoology*, 72, 37–52.

Britski, H.A., & Birindelli, J.L.O. (2008) Description of a new species of the genus *Leporinus* Spix (Characiformes: Anostomidae) from the Rio Araguaia, Brazil, with comments on the taxonomy and distribution of *L. parae* and *L. lacustris*. *Neotropical Ichthyology*, 6(1), 45–51.

Eigenmann, C. (1912) The freshwater fishes of British Guiana, including a study of the ecological grouping of the species and the relation of fauna of the plateau to that of the lowland. *Memoirs of the Carnegie Museum,* 5(1), i–xxii + 1–578, pls. 1–103.

Ferreira, E.J.G., Zuanon, J.A.S. & Santos, G.M. (1998) *Peixes comerciais do médio Amazonas: região de Santarém, Pará.* Edições IBAMA, Brasília, 211 pp.

Garavello, J.C. (1979) Revisão Taxonômica do Gênero *Leporinus* SPIX, 1829 (Ostariophysi, Anostomidae) Universidade de São Paulo, Instituto de Biociências, São Paulo, 451 pp.

Garavello, J.C. & Britski, H.A. (2003) Family Anostomidae. *In:* Reis, R.E., S.O. Kullander & C.J. Ferraris (Eds.), *Check list of the freshwater fishes of South and Central America*. Edipucrs, Porto Alegre, pp. 71–84.

Garavello, J.C. & Santos, G.M. (2009) Two new species of *Leporinus Agassiz*, 1829 from Araguaia-Tocantins system, Amazon basin, Brazil (Ostariophysi, Anostomidae). *Brazilian Journal of Biology*, 69(1), 109–116.

Géry, J. (1974) Notes sur quelques Anostomidae (Pisces, Characoidei) du bassin Amazonien. *Vie Milieu 1972-193,* 23(1), 143–175.

Géry, J. (1977) *Characoids of the world.* T.F.H. Publications, Neptune City, 672 pp.

Hammer, O, Harper, D.A.T. & Ryan, P.D. (2001) PAST: paleontological statistics software package for education and data analysis. *Palaeontol Electronica*, 4, 1–9.

Henn, A.W. (1928) List of types of fishes in the collection of the Carnegie Museum on September 1, 1928. *Annals of the Carnegie Museum*, 19, 51–99.

Ibarra, M. & Stewart, D.J. (1987) Catalogue of type specimens of recent fishes in Field Museum of Natural History. *Fieldiana Zoology*. 35, 1–112.

Jégu, M., Queiroz, L.J., Camacho-Terrazas, J., Torrente-Vilara, G., Carvajal-Vallejos, F.M., Poully, M. & Zuanon, J. (2012). Catálogo de los peces de la cuenca Iténez (Bolivia y Brasil), *In:* Van Damme, P.A., Maldonado, M., Poully, M. & Doria, C. R.C. (Eds.). *Águas del Iténez–Guaporé: recursos hidrobiológicos de un patrimonio binacional (Bolivia–Brasil).* INIA, Cochabamba, pp. 111–156.

Klingenberg, C.P., Barluenga, M. & Meyer, A. (2002) Shape analysis of symmetric structures: quantifying variation among individuals and asymmetry. *Evolution*, 56(10), 1909–1920.

Lasso, C.A., Lew, D., Taphorn, D., Nascimiento, C., Lasso- Alcalá, O., Provenzano, F. & Machado-Allison, A. (2004) Biodiversidad ictiológica continental de Venezuela. Parte 1. Lista de especies y distribución por cuencas. *Memoria Fundación La Salle de Ciencias Naturales*, 159–160, 105–195.

Machado-Evangelista, M., Esguícero, A.L.H., Arcifa, M.S. & Pereira, T.N.A. (2015) Diet and ecomorphology of *Leporinus reticulatus* (Characiformes: Anostomidae)

from the upper Rio Juruena, MT, Brazil: ontogenetic shifts related to the feeding ecology. *Acta Amazonica*, 45(4), 383–392

Mautari, K.C. & Menezes, N.A. (2006) Revision of the South American freshwater fish genus *Laemolyta* Cope, 1872 (Ostariophysi, Characiformes, Anostomidae). *Neotropical Ichthyology*, 4(1), 27–44.

Melo, B.F. (2015) Relações filogenéticas na superfamília Anostomoidea (Ostariophysi: Characiformes). Universidade Estadual Paulista Júlio de Mesquita Filho, Instituto de Biociências de Botucatu, Botucatu, 181 pp.

Myers, G.S. (1927) Descriptions of new South American freshwater fishes collected by Dr. Carl Ternetz. *Bulletin of theMuseum of Comparative Zoology at Harvard College*, 68(3), 107–135.

Myers, G.S. (1950) Studies on South American fresh-water fishes. II. The genera of Anostomine characids. *Stanford Ichthyological Bulletin*, 3(4), 185–197.

Ocampo, J.A.; Vari, R.P. & Usma, J.P. (2008) Checklist of the Freshwater Fishes of Colombia. *Biota Colombiana*, 9(2), 143–237.

Ohara, W.M., Lima, F.C.T., Salvador, G.N. & Andrade, M.C. (2017) *Peixes do Rio Teles Pires: diversidade e guia de identificação.* Museu de Zoologia da Universidade de São Paulo/Universidade Federal do Pará/Museu de Zoologia da Universidade Estadual de Campinas. São Paulo/Campinas, 399 pp

Pellegrin, J. (1909) Characinidés américains nouveaux de la collection du Muséum d'Histoire Naturelle. *Bulletin du Muséum National d'Histoire Naturelle*, 14(7), 342–347.

Feitosa, F.S. & Santos, G.M. (2013) Anostomoidae. *In:* Queiroz, L.J., Torrente-Vilara, G., Ohara, W.M., Pires, T.H.S., Zuanon, J.A.S. & Doria, C.R.C. (Eds.), *Peixes do Rio Madeira*, *Vol. 1*. Dialeto Latin America Documentary, São Paulo, 146–165pp.

Ramirez, J.L. (2015) Filogenia molecular dos Anostomidae e filogeografia das espécies com cromossomos sexuais ZZ/ZW do gênero *Leporinus*. Universidade Federal de São Carlos, Centro de Ciências Biológicas e da Saúde, São Carlos, 150 pp.

Ramirez, J.L., Birindelli, J.L.O. & Galetti, P.M. (2016) A New Genus of Anostomidae (Ostariophysi: Characiformes): Diversity, Phylogeny and Biogeography Based on Cytogenetic, Molecular and Morphological Data. *Molecular Phylogenetics and Evolution*, 107, 308–323.

Ramirez, J.L., Birindelli, J.L.O., Carvalho, D.C., Affonso, P.A.M., Venere, P.C., Ortega, H., Carrillo-Avila, M., Rodríguez-Pulido, J.A. & Galetti, P.M. (2017)

Revealing Hidden Diversity of the Underestimated Neotropical Ichthyofauna: DNA Barcoding in the Recently Described Genus *Megaleporinus* (Characiformes: Anostomidae). *Frontiers in Genetics*, 8, pp. 149.

Rodriguez, G. (1993) From Oviedo to Rathbun: The development of brachyuran crab taxonomy in the Neotropics (1535–1937). *In*: Truesdale, F. (Ed), *History of carcinology*. A. A. Balkema, Rotterdam and Brookfield, pp. 41–74.

Sabaj, M.H. (2016) Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an online reference. Version 6.5 (16 August 2016). American Society of Ichthyologists and Herpetologists, Washington, D.C., Electronic publication. Available from: http://www.asih.org/ (accessed 03 October 2018)

Santos, G.M, Jégu, M. & Merona, B. (1984) *Catálogo de peixes comerciais do baixo Rio Tocantins. Projeto Tucuruí.* Eletronorte-CNPq-INPA, Manaus, 83 pp.

Santos, G.M. & Jegu, M. (1989) Inventário taxonômico e redescrição das espécies de anostomídeos (Characiformes, Anostomidae) do baixo Rio Tocantins, PA, Brasil. *Acta Amazônica*, 19, 159–213.

Santos, G.M. & Jegu, M. (1996) Inventário taxonômico dos Anostomídeos (Pisces, ANOSTOMIDAE) da bacia do Rio Uatumã- AM, Brasil, com descrição de duas espécies novas. *Acta Amazonica*, 26(3), 151–184.

Santos, G.M., Merona, B., Juras, A.A. & Jegú, M. (2004) *Peixes do Baixo Tocantins: 20 anos depois da Usina Hidrelétrica de Tucuruí*. Eletronorte, Brasília, 215 pp.

Santos, G.M. & Zuanon, J.A.S. (2006) *Anostomoides passionis*, a new fish species from Rio Xingu, Brasil (Characiformes: Anostomidae). *Zootaxa,* 1168, 59–68.

Santos, G.M., Ferreira, E.J.G. & Zuanon, J.A.S. (2006) *Peixes Comerciais de Manaus.* ProVárzea, Ibama/AM, Manaus, 144 pp.

Sarmiento, J., Bigorne, R., Carvajal-Vallejos, F.M., Maldonado, M., Leciak, E. & Oberdorff, T. (2014) *Peces de Bolivia/Bolivian fishes*. Plural editores, Bolívia, 211 pp.

Sidlauskas, B. & Vari, R.P. (2008) Phylogenetic relationships within the South American fish family Anostomidae (Teleostei, Ostariophysi, Characiformes). *Zoological Journal of the Linnean Society,* 154(1), 70–210.

Sidlauskas B., Mol, J.H. & Vari R. P. (2011) Dealing with allometry in linear and geometric morphometrics: a taxonomic case study in the *Leporinus cylindriformis*

group (Characiformes: Anostomidae) with description of a new species from Suriname. *Zoological Journal of the Linnean Society*, 162(1), 103–130.

Sidlauskas, B.L. & Vari, R.P. (2012) Diversity and distribution of anostomoid fishes (Teleostei: Characiformes) throughout the Guianas. *Cybium*. 36(1), 71–103.

Sidlauskas, B. & Birindelli, J.L.O. (2017). Family Anostomidae – Toothed headstanders. *In*: Van der Sleen, P. & Albert, J.S. (Eds.), *Field guide to the fishes of the Amazon, Orinoco and Guyanas*. Princeton University Press, New Jersey, pp. 82–89.

Steindachner, F. (1876) Ichthyologische Beiträge (V). Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. *Mathematisch-Naturwissenschaftliche Classe*, 74, 49–240.

Taylor, W.R. & Van Dyke, G.C. (1985) Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium*, 9(2), 107–119.

Vari, R.P. & Williams, A.M. (1987) Headstanders of the Neotropical anostomid genus *Abramites* (Pisces: Characiformes: Anostomidae). *Proceedings of the Biological Society of Washington*, 100(1), 89–103.

Weitzman, S.H. (1962) The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family. *Stanford Ichthyogical Bulletin*, 8(1), 3–77.

Weitzman, S.H. (1974) Osteology and evolutionary relationships of the Sternoptychidae, with a new classification of stomiatoid families. *Bulletin of the American Museum of Natural History*. 153(3), 327–478.

Winterbottom, R. (1980) Systematics, osteology and phylogenetic relationships of fishes of the ostariophysan subfamily Anostominae (Characoidei, Anostomidae). *Life SciencesContributions: Royal Ontario Museum*, 123, 1–112.

- Capítulo 2-

Testing the monophyly of *Anostomoides*, with description of a new genus of Anostomidae (Characiformes)

Artigo formatado nas normas do periódico Zoologica Scripta

Testing the monophyly of *Anostomoides*, with description of a new genus of Anostomidae (Characiformes)

Abstract

Anostomidae is the second most diverse family of the Characiformes. However, much is still poorly understood in the taxonomy and phylogeny of the species of the group. *Anostomoides* is one of the 15 genera of Anostomidae and it encompasses only two valid species, according to the recently published taxonomic revision. *Anostomoides atrianalis*, the type species, is a more widespread species occurring in the Amazon, Orinoco, and Essequibo drainages, wheras *A. nattereri* is distributed in the Amazon basin. The phylogenetic relationships of these species are poorly understood. The aim of the present contribution is to study the phylogenetic relationships of these two species among Anostomidae, testing the genus monophyly. For that, two independent phylogenetic analyses were performed, one including 123 morphological characters coded for 48 species of Anostomidae representing almost all genera and another using five gene sequences obtained in GenBank or originally sequenced. Our results strongly support the poliphyly of *Anostomoides*, as previously defined. Therefore, a new genus is detailed described and illustrated to allocate *A. nattereri*. In addition, the main characters supporting the phylogenetic relationships of the new genus are discussed.

Key-words. Phylogeny; Anostomoidea; South America; *Anostomus*.

Resumo

Anostomidae é a segunda família de Characiformes mais diversa. Entretanto, há ainda muito o que se conhecer sobre a taxonomia e filogenia das espécies deste grupo. *Anostomoides* é um dos 15 gêneros de Anostomidae e inclui apenas duas espécies válidas, de acordo com a revisão taxonômica recentemente publicada. *Anostomoides atrianalis*, a espécie tipo do gênero, é mais amplamente distribuída ocorrendo nas drenagens dos rios Amazonas, Orenoco e Essequibo,

enquanto que *A. nattereri* distribui-se na bacia Amazônica. As relações filogenéticas entre estas espécies são pouco conhecidas. O objetivo do presente estudo é investigar as relações filogenéticas destas duas espécies, testando o monofiletismo do gênero. Para isso, duas análises filogenéticas independentes foram realizadas, a primeira com base em 123 caracteres morfológicos codificados para 48 espécies que representam quase todos os gêneros, e a segunda usando sequências de cinco genes obtidas no GenBank ou originalmente. Nossos resultados corroboram o polifiletismo de *Anostomoides*, como previamente definido. Portanto, um gênero novo é detalhadamente descrito e ilustrado para abrigar *A. nattereri*. Além disso, os principais caracteres que suportam as relações filogenéticas do gênero novo são discutidos.

Palavras-chave. Filogenia; Anostomoidea; América do Sul; *Anostomus*.

Introduction

Anostomidae is the second most diverse family of the Characiformes (Nelson, Grande & Wilson, 2016), with approximately 155 valid species, distributed in 15 genera (Ramirez et al., 2017). The anostomids are relatively abundant and widely distributed in South America, from north of Colombia to temperate Argentina (Garavello & Britski 2003), occurring in all major basins, including Amazonas, Uruguay, Paraná, Paraguay, Orinoco, Essequibo, São Francisco, Magdalena and Maracaibo lake, as well as the smaller basins of eastern and northeastern Brazil, Guyanas basins, Suriname, and eastern Ecuador.

Between the years of 1885 and 1886, Jean Chaffanjon and his team collected, in the Orinoco river in Venezuela, three specimens of Anostomidae with a slightly upturned mouth, possibly intemediary between genera *Leporinus* Agassiz 1829 and *Anostomus* Scopoli 1777 (Pelegrin, 1909). Based on these specimens, Pelegrin (1909) described the genus *Anostomoides* to allocate his new species: *A. atrianalis*.

Few years later, Eigenmann (1912) described *Schizodontopsis laticeps*, based on specimens collected in the Essequibo river at Crabs Falls in Guyana. The species was later transferred to *Anostomoides laticeps* (Géry, 1974). These two species of *Anostomoides* remained known only for their types for many decades. More recently, Santos & Zuanon (2006) described *Anostomoides passionis* as a species endemic to the rapids of the Xingu river in Brazil. The taxonomy of the group was only recently assessed (Assega & Birindelli, 2019) and currently *Anotomoides* includes only two valid species: *A. atrianalis* (senior synonym of *A. laticeps*) and *A. nattereri* (senior synonym of *A. passionis*). The later valid species was described in *Leporinus* by Steindachner, remained poorly known until now, and transferred to *Anostomoides* by Assega & Birindelli (2019).

The validity of *Anostomoides* was debated in the 20th century, first when Borodin (1931) considered it a subgenus of *Schizodontopsis* (=*Laemolyta*), and then when Myers (1950) considered it as a taxon with insufficient information to delimit its validity. Géry (1974) resurrected *Anostomoides* limiting his comments to a footnote, mentioning it as distinct from *Laemolyta* Cope 1872.

The phylogenetic relationships of *Anostomoides* are also insufficiently studied. In a comprehensive phylogenetic analysis based on morphology, Sidlauskas & Vari (2008) recovered *Anostomoides atrianalis* as sister group to Anostominae (*Anostomus* Scopoli 1777*, Gnathodolus* Myers 1927*, Petulanus* Sidlauskas & Vari 2008*, Pseudanos* Winterbottom 1980*, Sartor* Myers & Carvalho 1959 and *Synaptolaemus* Myers & Fernández-Yépez 1950,) plus *Rhytiodus* Kner 1858, *Schizodon* Agassiz 1829 and *Laemolyta* Cope 1872. More recently molecular-based analyses, proposed by Melo (2015) and Ramirez (2015), showed *Anostomoides atrianalis* as sister group to *Laemolyta, Rhytiodus* and *Schizodon*, whereas Anostominae was considered as more closely related to *Leporellus*, at the insertion of the anostomid tree. However, no studies so far have included *A. nattereri*, therefore no test of the monophyly of *Anostomoides* was ever performed.

104 The aim of the present contribution is to investigate the phylogenetic relationships of the
105 two species of *Anostomoides*, based on morphology and molecules, thus testing the genus
106 monophyly. As a result, a new genus exclusively to allocate *A. nattereri* is diagnosed, described,
107 and illustrated.
108
109 **Material and methods**
110 **Osteological preparations and Terminology**
111 Specimens were cleared and double stained (cs) following Taylor & Van Dyke (1985), or
112 prepared as dry skeletons according to Bemis *et al*. (2004). Dissections followed the technique
113 described by Weitzman (1974). Osteological nomenclature follows Weitzman (1962), except for
114 the following cases. Entopterygoid is used instead of mesopterygoid, following Arratia (1992).
115 Anterior and posterior ceratohyal is used instead of ceratohyal and epihyal, following Vari (1983).
116 Institutional abbreviations for fish collections follow Sabaj (2016).
117
118 **Morphological Phylogeny**
119 To the character matrix of Sidlauskas & Vari (2008), which included 46 species
120 representing 14 genera (all except *Megaleporinus*) and approximately one third of species
121 diversity of Anostomidae, to which *Leporinus scalabrinni* Ameghino 1898, was later added by
122 Bogan, Sidlauskas, Vari & Agnolin (2012), we added *A. nattereri*, for which we coded all the 123
123 characters described in the original study (Table 1). Additionally, the character codification for *A.*
124 *atrianalis* was reviewed based on additional specimens (Table 2, and see Comparative Material).
125 Fourteen outgroup taxa were included, and Distichodontidae was used as tree root, following
126 Sidlauskas & Vari (2008). The data matrix was assembled in Mesquite v. 1.12 (Maddison &
127 Maddison, 2017). Phylogenetic analysis based on morphological characters was obtained by
128 parsimony analysis using TNT software version 1.1 (Goloboff, Farris & Nixon, 2008). Following

Sidlauskas & Vari (2008), all characters were considered as non-additive and receveid equal weights. One thousand heuristic searches were undertaken, using tree bisection–reconnection (TBR), and the program set to collapse branches of zero length. A strict consensus tree was calculated from resulting trees. Consistency (CI) and Retention (RI) indices of fundamental trees and strict consensus were also calculated using TNT, through the script 'stats'.

Table 1. Character states for 123 characters of *Anostomoides atrianalis*. Characters based on Sidlauskas & Vari (2008).

1100201201 0000101100 0110011000 4231040000 1110110110 0000000001 1100101100 0110110001 0011001011 1001210000 0000101100 0100001101 000

Table 2. Character states for 123 characters of *New genus*. Characters based on Sidlauskas & Vari (2008).

0000101200 1000001111 0010000000 4110140010 0120110110 0000000001 1100010010 0110010000 0011001010 1101210001 0000011100 0100000100 000

Molecular Phylogeny

We used sequences from 29 species belonging to 11 genera of Anostomidae compiled from GenBank along with four outgroup species belonging to Chilodontidae, Curimatidae, Prochilodontidae and *Hemiodus unimaculatus* (Bloch 1794) (Hemiodontidae), latter used for rooting the trees (Table 3). In case of multiple individuals of the same species, the taxon presenting the most complete sequence was chosen and the others discarded.

DNA extractions from muscle or fins were carried out using a DNeasy Tissue kit (Qiagen Inc.) following manufacturer's instructions. We amplified partial sequences of the two

mitochondrial genes *cytochrome oxidase c subunit I* (*COI*, 630 bp) and *cytochrome b* (*Cytb*, 1,005 bp) and three nuclear genes *myosin heavy chain 6 gene* (*Myh6*, 750 bp), *recombination activating gene 1* (*Rag1*, 1,317 bp), and *recombination activating gene 2* (*Rag2*, 1,020 bp). Primer sequences were obtained from the literature (Palumbi, 1996; Lovejoy & Collette, 2001; Li, Ortí, Zhang & Lu, 2007; Melo, Benine, Mariguela & Oliveira, 2011; Abe, Mariguela, Avelino, Castro & Oliveira, 2013). We used 12.5 µl as a total volume with 9.075 µl of double-distilled water, 1.25 µl 5x reaction buffer, 0.375 $MgCl_2$, 0.25 µl dNTP mix at 8 mM, 0.25 µl of each primer at 10 µM, 0.05 µl Platinum Taq DNA polymerase enzyme (Invitrogen; www.invitrogen.com) and 1.0 µl genomic DNA (10–50 ng). PCR parameters consisted of an initial denaturation (4 min at 95ºC) followed by 28-30 cycles of chain denaturation (30 s at 95ºC), primer hybridization (30–60 s at 52–54ºC), and nucleotide extension (30–60 s at 72ºC). Fragments were vizualized using 1% agarose gel and the PCR product was cleaned using ExoSAP. Sequencing followed using dye terminators (BigDye™ Terminator v 3.1 Cycle Sequencing Ready Reaction Kit, Applied Biosystems) and purified through ethanol precipitation. We then sequenced the samples on an automatic sequencer ABI 3130-Genetic Analyzer (Applied Biosystems) at the Universidade Estadual Paulista Júlio de Mesquita Filho, Botucatu.

We assembled and edited consensus gene sequences in Geneious v11.1.2 (Kearse et al., 2012) and aligned using the Muscle algorithm (Edgar, 2004). We used the concatenated matrix to run maximum likelihood (ML) searches using a random starting tree with GTRGAMMA model (Stamatakis, Hoover & Rougemont, 2008) through RAxML 7.2.8 (Stamatakis, 2006) as implemented on Geneious 11.1.2. All other parameters are left at default. One thousand bootstrap pseudoreplicates tested the support for each node.

170 **Table 3.** Voucher information and GenBank accession numbers for specimens included in the analyses.

Species	River	Basin	Catalog number	COI	Cytb	RAG1	RAG2	Myh6
Abramites hypselonotus	Madeira	Madeira	UFRO-I 8234*	KF568968	KF569013	KF569056	KF569099	KF569142
Abramites hypselonotus	Yarinacocha	Amazonas	MUSM 47356	KU134848	KU134866	KU134884	KU134902	KU134920
Anostomoides atrianalis	Caura	Amazonas	AUM 53813					
Anostomoides atrianalis	Nanay	Amazonas	FMNH 123875					
Anostomoides atrianalis	Aripuanã	Amazonas	UNIR8702					
Anostomus ternetzi	Arinos	Tapajós	MZUSP 113996	KF568970	KF569013	KF569056	KF569099	KF569142
Anostomus ternetzi	Jamanxim	Tapajós	MZUSP 97271					
Hypomasticus megalepis	Pitinga	Uatumã	MZUEL 10200	KX020571	KX020574	KX020580	KX020583	KX020577
Hypomasticus mormyrops	Bananal	Paraíba do Sul	MZUEL 08022	KX020572	KX020575	KX020581	KX020584	KX020578
Hypomasticus pachycheilus	Madeira	Madeira	UFRO-I 2156	KF568973	KF569016	KF569059	KF569102	KF569145
Laemolyta fernandezi	Tocantins	Araguaia	GEPEMA-5598	KF568974	KF569017	KF569060	KF569103	KF569146
Laemolyta proxima	Madeira	Madeira	UFRO-I 4043					
Leporellus cf. *vittatus*	Cataniapo	Orinoco	AUM 54212					
Leporellus vittatus	Salto das nuvens	Sepotuba	MZUSP 113987	KF568980	KF569023	KF569066	KF569109	KF569152
Leporellus vittatus	Paraná	La Plata	LBP 1669					
Leporinus copelandii	Manhuaçu	Doce	MCNIP 0459	KF568978	KF569021	KF569064	KF569107	KF569150
Leporinus fasciatus	Madeira	Madeira	UFRO-I 3343	KF568981	KF569024	KF569067	KF569110	KF569153
Leporinus friderici	Turvo	Paraná	MZUSP 113983	KF568982	KF569025	KF569068	KF569111	KF569154
Leporinus lacustris	Cuiabá	Paraguay	MZUSP 113991	KF568985	KF569028	KF569071	KF569114	KF569157
Leporinus steindachneri	Jequitinhonha	Jequitinhonha	MCNIP 0379	KF568994	KF569037	KF569080	KF569123	KF569166
Leporinus striatus	Salto das nuvens	Sepotuba	MZUSP-113986	KF568995	KF569038	KF569081	KF569124	KF569167
Megaleporinus elongatus	Itacambiruçu	Jequitinhonha	MCNIP 0375	KU134853	KU134871	KU134889	KU134907	KU134925
Megaleporinus macrocephalus	Cuiabá	Paraguay	MZUSP 118667	KU134856	KU134874	KU134892	KU134910	KU134928
Megaleporinus obtusidens	Jacuí	Jacuí	MCP 25476	KU134859	KU134877	KU134895	KU134913	KU134931
Megaleporinus trifasciatus	Ucayali	Amazonas	MUSM 47351	KU134865	KU134883	KU134901	KU134919	KU134937

New genus	Bacajaí	Xingu	MZUSP 110595					
New genus	Iriri	Xingu	INPA 40009					
New genus	Xingu	Xingu	INPA 40753					
New genus	Xingu	Xingu	INPA 40840					
Pseudanos trimaculatus	Cautário	Madeira	UFRO-I 14970	KF569003	KF569046	KF569089	KF569132	KF569175
Rhytiodus lauzannei	Madeira	Madeira	UFRO-I 6840	KF569005	KF569048	KF569091	KF569134	KF569177
Rhytiodus microlepis	Madeira	Madeira	UFRO-I 18647	KF569004	KF569047	KF569090	KF569133	KF569176
Schizodon borellii	Cuiabá	Paraguay	MZUSP 113990	KF569006	KF569049	KF569092	KF569135	KF569178
Schizodon fasciatus	Guaporé	Madeira	MZUSP 113989	KF569007	KF569050	KF569093	KF569136	KF569179
Schizodon intermedius	Tiete	Paraná	MZUSP 113995	KF569008	KF569051	KF569094	KF569137	KF569180

Results

[genus name], new genus

Type species by monotypyc: *Leporinus nattereri* Steindachner 1876.

Diagnosis

The new genus is diagnosed among Anostomidae, except Anostominae, by having dermal papillae on upper and lower lips (Fig. 1; *vs.* dermal papillae absent), and by lacking a lateroanterior process on the palatine (Figs. 3–4; *vs*. palatine bearing a lateroanteriorly directed process). The new genus is diagnosed by Anostominae by having slightly upturned mouth in specimens larger than 100 mm SL (*vs*. distinctly uptuned mouth in all specimens).

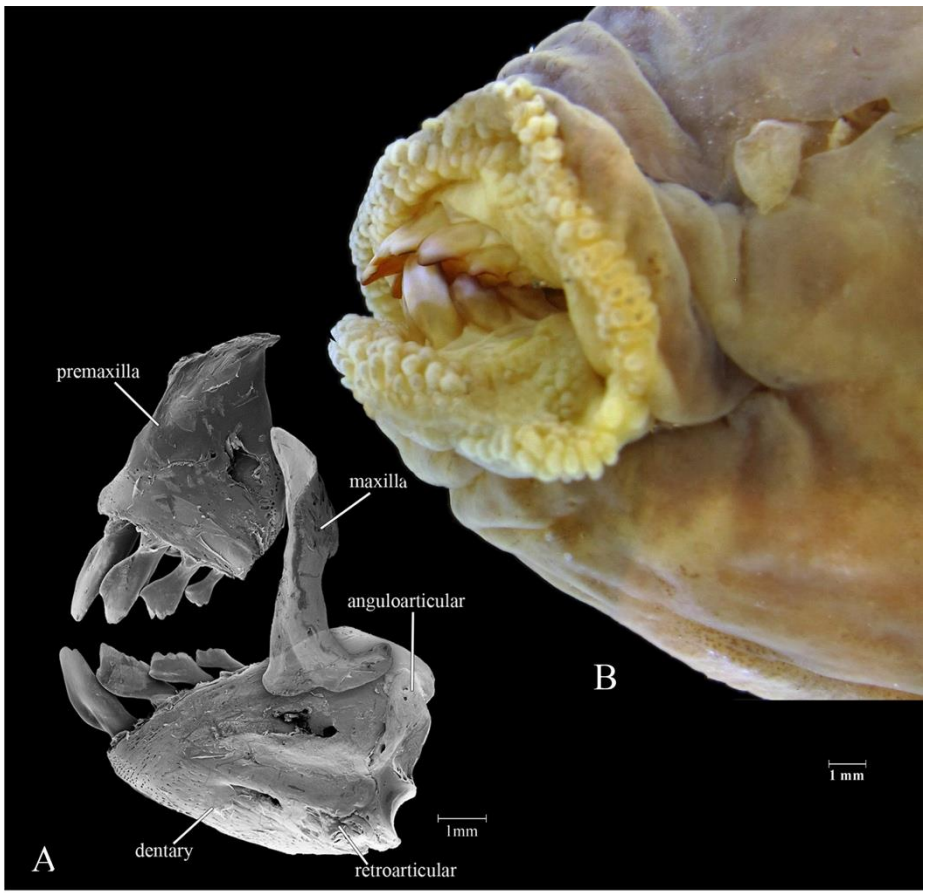


Figure 1. Scanning electron microscope image of left upper and lower jaws of "*Anostomoides*" *nattereri*, MZUSP 5429, 89.0 mm SL (A) and lips and teeth in detail of "*Anostomoides*" *nattereri*, FMNH 103451, 141.8 mm SL (B).

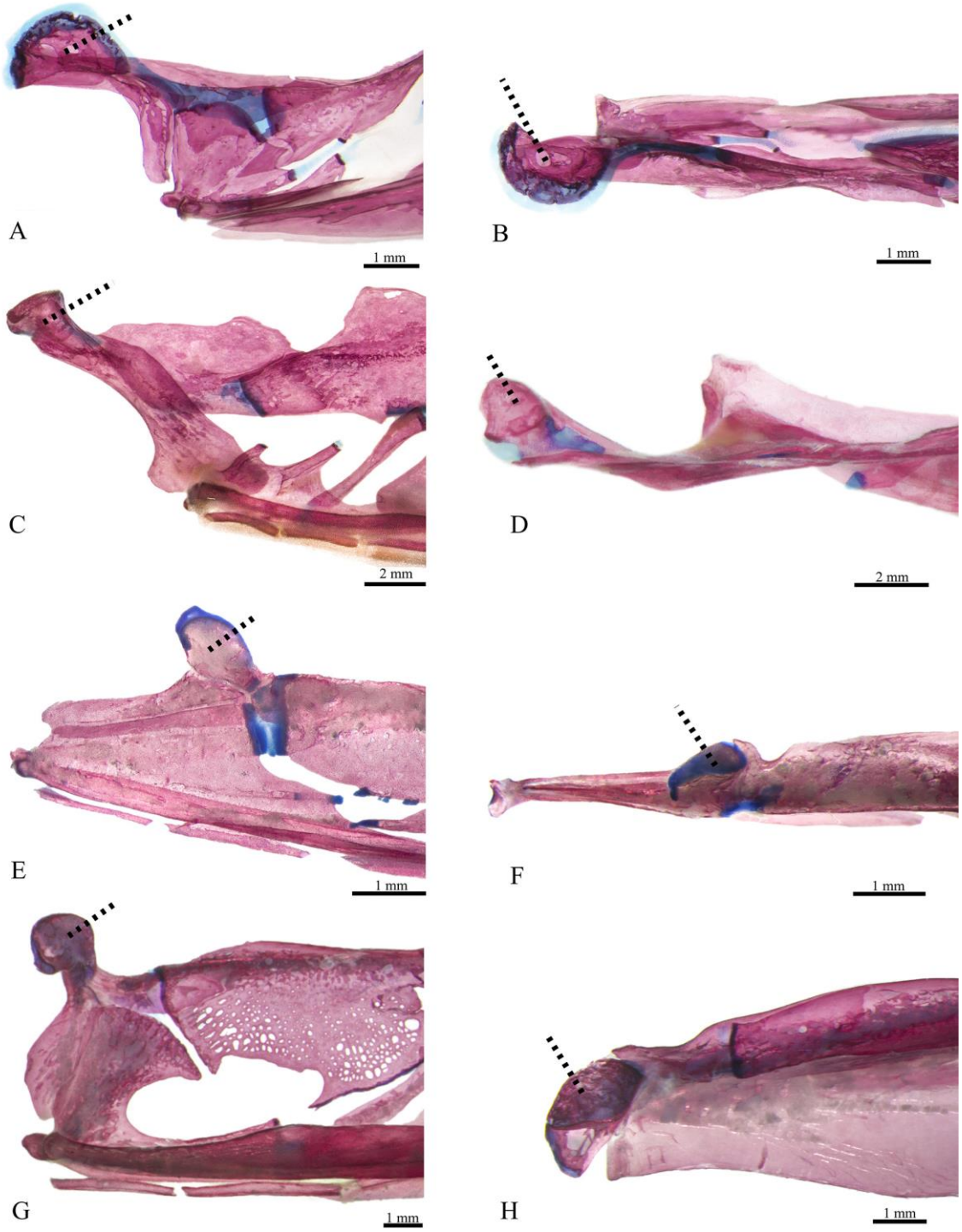
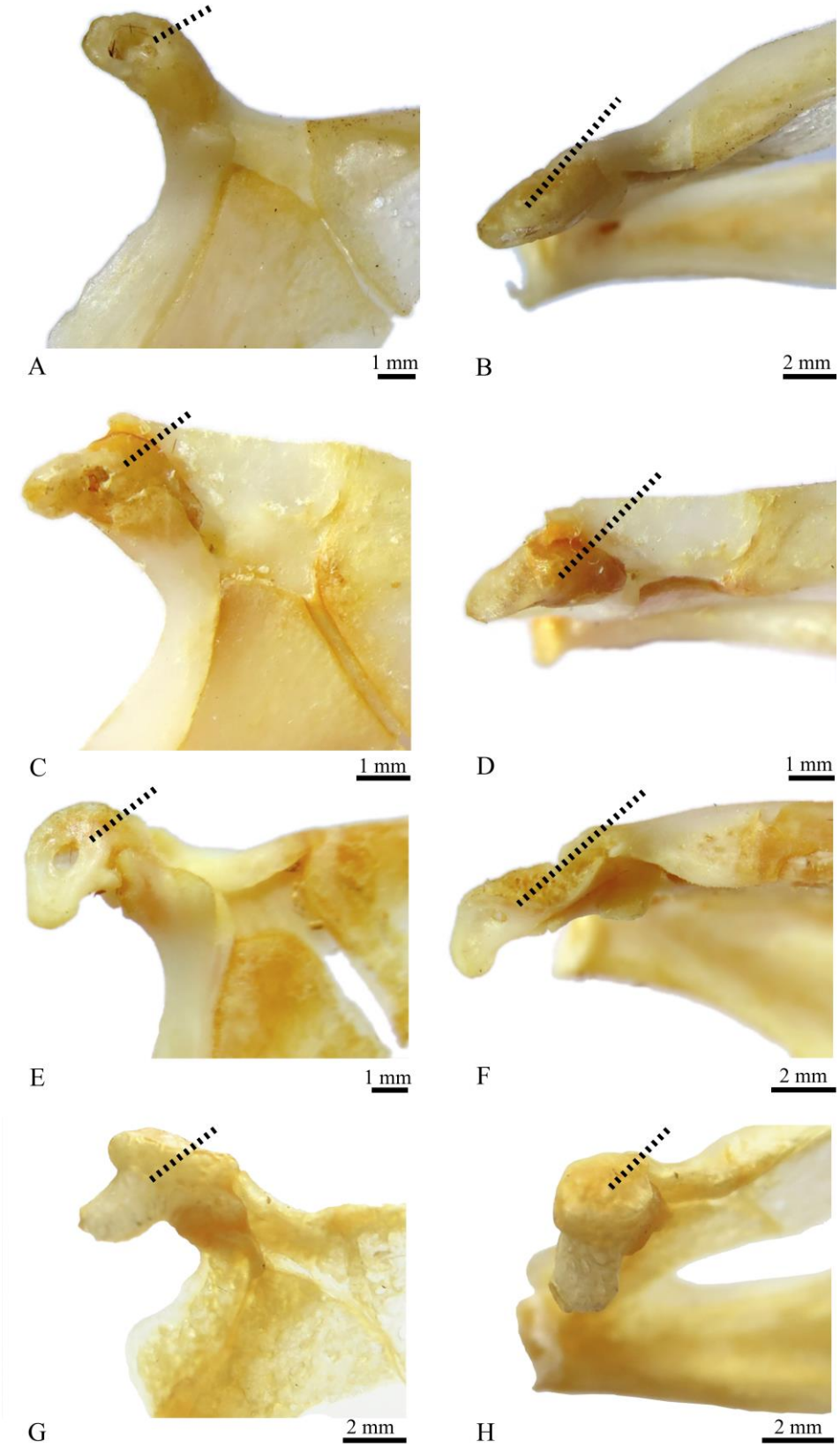


Figure 2. Detail of Palatine in lateral (left) and dorsal (right) views of: (A and B) *Caenotropus labyrinthicus*, MZUSP29351, 68.9 mm SL; (C and D) *Prochilodus nigricans*, MZUSP 95799, 112.5 mm SL; (E and F) *Petulanos intermedius,* MZUSP 97330, 59.6 mm SL; (G and H) *Anostomoides atrianalis*, ANSP159599, 159.6 mm SL.



192

193 **Figure 3.** Detail of Palatine in lateral (left) and dorsal (right) views in skeleton of: (A and B)
194 *"Anostomoides" nattereri*, MZUSP110595, 232.0 mm SL; (C and D) *Leporellus vittatus*, MZUSP 106332,
195 155.0 mm SL; (E and F) *Leporinus obtusidens,* MZUEL 16470, 260.0 mm SL; (G and H) *Anostomoides*
196 *atrianalis*, MZUSP 67269, 218.0 mm SL.

The new genus can be further distinguished from *Abramites* and *Megaleporinus* by having four teeth on the premaxillary and dentary bones (*vs*. three); from *Laemolyta* and *Schizodon* by having the two medial premaxillary teeth with one or two cusps (*vs*. premaxillary teeth with four or fives cusp); from *Anostomoides* by having four branchiostegal rays (*vs*. three) and 37 to 39 lateral line scales (*vs*. 41 to 44); from *Rhytiodus* by having 37 to 39 lateral line scales (*vs*. 48 to 92); from *Hypomasticus* and *Leporinus* by having slightly upturned mouth in specimens larger than 100 mm SL (*vs*. mouth downturned or terminal in specimens larger than 100 mm SL); and from *Leporellus* by having slightly upturned mouth (*vs*. downturned mouth), caudal-fin rays naked (*vs*. medial third of caudal-fin rays covered by scales) and caudal fin uniformely colored (*vs*. caudal fin with three to seven dark longitudinal stripes).

Description

For information regarding general body shape, description of external features, morphometrics, and meristics (including counts of rays and scales and teeth), see Assega & Birindelli (2019).

Osteology

Infraorbital bones and associated elements. Infraorbital series composed by six plate-like bones (Fig. 4). Infraorbital 1 deep, rounded margin, with its ventral portion larger than dorsal portion; sensory canal slightly vertical, with lower half bended posteriorly, bearing three equidistant pores and located on ventral portion of infraorbital. Infraorbital 2 elongate, length approximately three times depth, with irregular margin; sensory canal more or less longitudinal, bearing one pore on anterior tip, an intermediate pore and a pore on posterior tip. Infraorbital 3 elongated, abbreviated *C*-shaped with irregular margins, length twice depth, one pore on each extremity. Infraorbital 4

vertical, deep, with depth twice length; sensory canal *Y*-shaped bearing three pores, with posterior pore on dorsal portion of posterior margin.

Figure 4. Infraorbital bones and associated elements of "*Anostomoides*" *nattereri*, MZUSP 5429, 138.7 mm SL. **Ant:** antorbital, **Io1-6:** infraorbital, **Na:** nasal, **So:** supraorbital

Infraorbital 5 deep, with depth twice length, inclined with ventral portion more posterior than dorsal one, with irregular margin; sensory canal straight with two pores, one at each dorsal and ventral tips. Infraorbital 6 approximately ovate, inclined more longitudinal than vertical with dorsal portion anteriorly oriented; sensory canal shorter than bone, *Y* shaped, bearing three pores, two on dorsal tip. Anterorbital relatively thin, more or less straight, inclined with anterior portion anteriorly directly, posterior portion acute; sensory canal absent. Supraorbital plate-like, inclined in the same direction as antorbital; sensory canal absent. Nasal plate-like, inclined as antorbital and supraorbital, bearing straight sensory canal with four equidistant pores.

Suspensorium and jaws. Quadrate triangular with large invagination in posterior margin, forming the quadrate-metapterygoid window; condyle of articular bone on anteroventral portion lateral face with large horizontal bony shelf for adductor mandibulae extended posterior (length almost twice length of remaning quadrate) (Fig. 5). Ectopterygoid vertical, depth three times

length, contacting palatine dorsally and posteriorly quadrate. Palatine shaped as a bean, contacting ectopterygoid and mesopterygoid, without median process (as in most Anostomidae, Sidlauskas & Vari, 2008: fig. 41). Unossified tissue, partially cartilaginous, on medial face of palatine. Mesopterygoid small on lateral face, slightly larger on medial face and sutured to metapterygoid. Metapterygoid shaped as half circle with straight dorsal border and anteroventral invagination for quadrate-metapterygoid window.

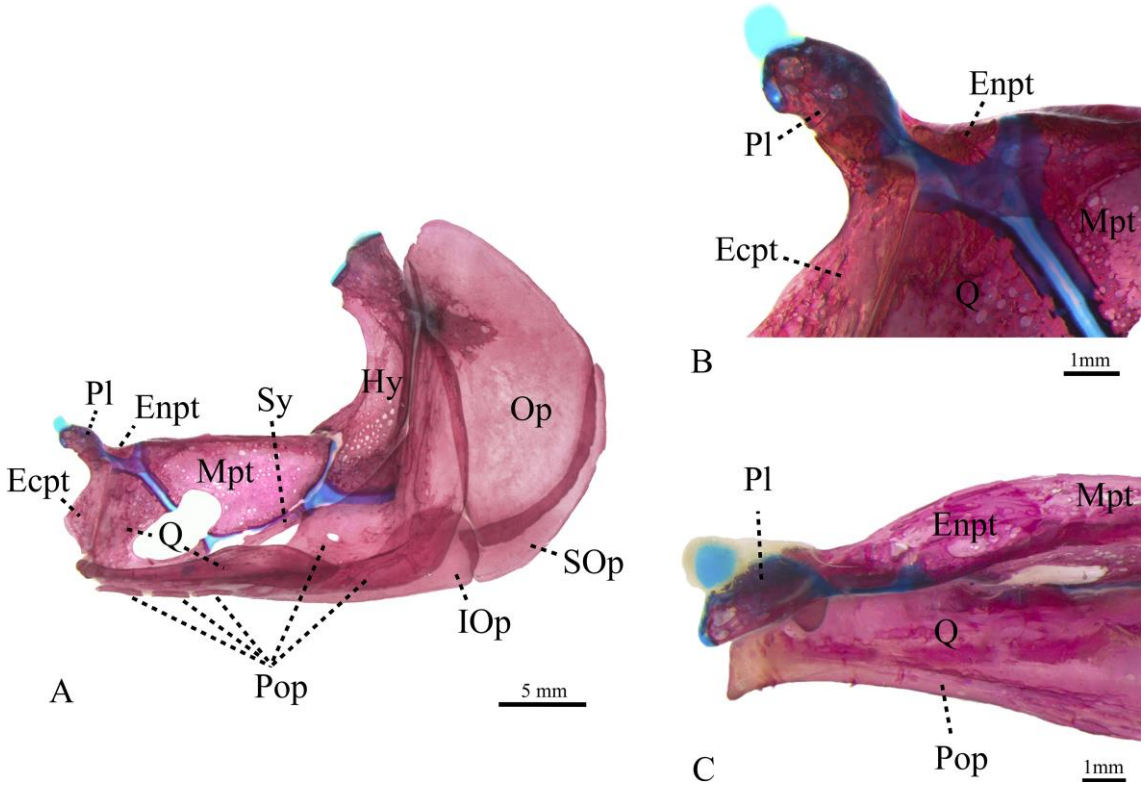


Figure 5. Suspensorium and jaws of "*Anostomoides*" *nattereri*, MZUSP 5429, 138.7 mm SL. **Ecpt:** ectopterygoid, **Enpt:** entopterygoid, **Hy:** hyomandibular, **IOp:** interopercle, **Mpt:** metapterygoid, **Op:** opercle, **Pl:** palatine, **Pop:** preopercle, **Q:** quadrate, **SOp:** subopercle, **Sy:** symplectic.

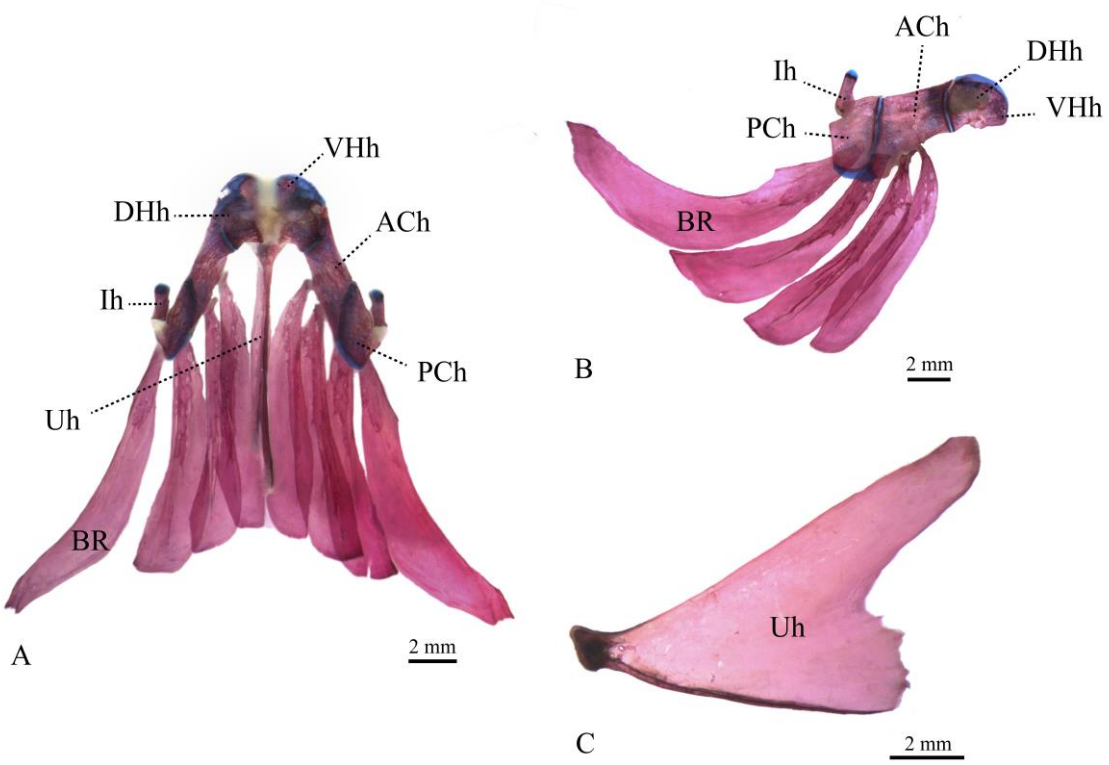
Sympletic small, plate-like and inclined, located between metapterygoid and preopercle. Preopercle large, shaped as an inverted *C*, with an opening near sympletic, bearing an inverted *L*-shaped sensory canal with five pores. Sensory canal continued anteriorly toward lower jaw, passing through three ossifications. Hyomandibular vertical, depth three length, shaped as an inverted *C*, with two condyles dorsally, and many small openings on ventral portion.

Opercle semicircular, with more or less straight anterior margin, posteroventral margin overlapping suborpercle, sickle shaped with blunt anterior margin. Interopercle rounded, acute anteriorly.

Lower jaw trapezoid to triangular, acute anteriorly, with condyle on posteroventral portion of jaw. Dentary large, anguloarticular vertical, with dorsal flange of moderate size (Fig. 1). Upper jaw formed by edentulous maxillary bone, with acute dorsal tip and large ventral tip, posteriorly extended, overlapping dentary ventrally, and overlapped by premaxillary bone dorsally.

Premaxillary bone trapezoid to triangular, with small dorsal process bent posteriorly, median process small linking counterpart premaxillary bone. Four premaxillary teeth, symphyseal teeth larger, wider, border slightly convex, remaining teeth slightly tricuspid with medial cusp distinctly larger or with blunt cutting edge. Four dentary teeth gently decreasing in size laterally, two medial teeth with truncate cutting edge without cusps, and two lateral teeth with three to five small cusps.

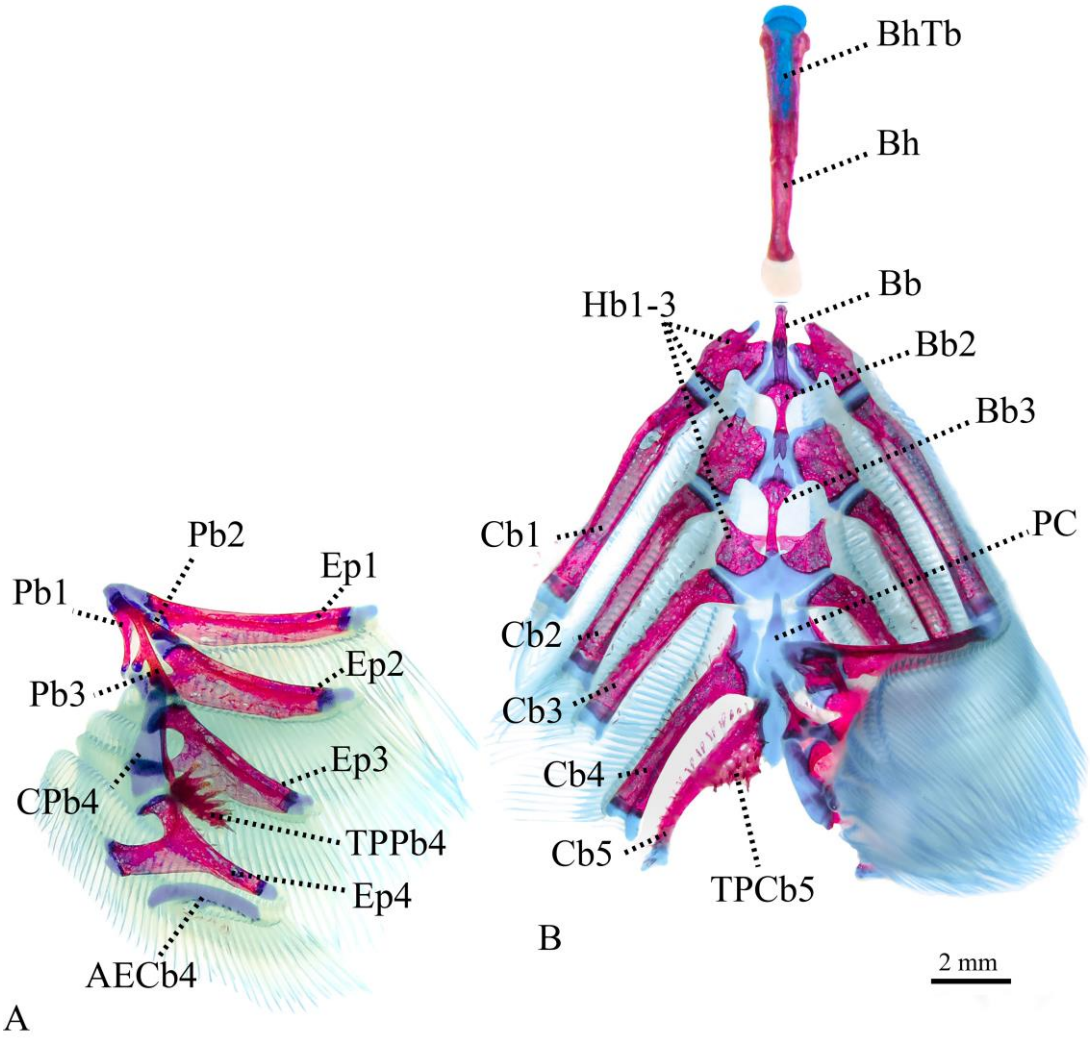
Hyoid arch. Dorsal hypohyal larger than ventral hypohyal, possessing a foramen (Fig. 6). Anterior ceratohyal larger than posterior ceratohyal, with anteroventral extension sutured to dorsal hypohyal. Four branchiostegal plate-like rays gradually larger posteriorly. Urohyal large, triangular, with straight dorsal and ventral margins, and irregular concave posterior margin. Interhyal small, rod-like.



275

276 **Figure 6.** Hyoid arch of "*Anostomoides*" *nattereri*, MZUSP 5429, 138.7 mm SL. **ACh:** anterior ceratohyal,
277 **BR:** branchiostegal rays, **DHh:** dorsal hypohyal, **Ih:** interhyal**, PCh:** posterior ceratohyal**, Uh:** urohyal**,**
278 **VHh:** ventral hypohyal.
279

280 **Branchial arches.** Basihyal elongate, rod-like, anterior half partially cartilaginous with anterior
281 margin rounded; posterior half completely ossified; dorsaly margin contacting edentulous basihyal
282 toothplate (Fig. 7). Three ossified basibranchial, small, interconnected by cartilage, first one small
283 and rod-like, basibranchials 2 and 3 rod-like except for triangular anterior tip.



284

285 **Figure 7.** Branchial apparatus of "*Anostomoides*" *nattereri* MZUSP 5429, 138.7 mm SL. **AECb4:**
286 accessory element of ceratobranchial 4, **Bb1–3:** basibranchial 1–3, **Bh:** basihyal, **BhTp**: basihyal
287 toothplate, **Cb1-5**: ceratobranchial 1-5, **Ep1–4:** epibranchial 1–4, **Hb1-3**: hypobranchial 1-3, **Pb1–4**:
288 pharyngobranchial 1–4**, PC:** posterior copula; **TPPb4:** tooth plate of fourth pharyngobranchial, **TPCb5:**
289 tooth plate of fifth ceratobranchial.
290

291 Posterior copula (also known as basibranchial 4 cartilage (Mattox, Britz & Toledo-Piza,
292 2016)) elongate, cartilaginous, plate-like anteriorly and rod-like posteriorly. Three ossified
293 hypobranchial dorsoventrally flattened, with cartilaginous tips, and laterally attached to respective
294 ceratobranchials. Hypobranchial 1 medially attached to basibranchials 1 and 2, bearing an
295 anteromedially directed cartilaginous tip. Hypobranchial 2 attached medially with basibranchials 2
296 and 3, bearing an anteromedially directed carilagenous tip. Hypobranchial 3 with acute tip
297 anterolaterally directed, posteriorly connected via cartilage to basibranchial 3.

Five ossified ceratobranchial, rod-like and elongate, posteriorly attached to respectively epibranchial (except for fifth ceratobranchial). Two rows of gill rakers on first three ceratobranchials and one anterior row of gill rakers in forth and fifth ceratobranchials. Fifth ceratobranchial with anterior portion expanded with one irregular row of teeth on dorsal surface.

Four ossified epibranchials, lacking gill rakers. First epibranchial rod-like, with slightly bifurcated medial tip. Second epibranchial *Y*-shaped. Third epibranchial with posterior bony extension and distinct uncinate process. Fourth epibranchial with uncinate process larger than medial tip. First pharyngobranchial with small dorsoposterior process and ventrolateral articulate with epibranchial 1. Second pharyngobranchial with small dorsolateral process ending in a cartilaginous tip, attached anteriorly with first pharyngobranchial 1, anteromedial attached with epibranchial 1 and posteriorly articulate with anterior margin of the pharyngobranchial 3. Third pharyngobranchial with small dorsolateral process, ending in cartilaginous tip, attached dorsomedial with ceratobranchial 2, posterolateral with ceratobranchial 3 and posteriorly with pharyngobranchial 4. Fourth pharyngobranchial articulate anteriorly with pharyngobranchial 3, anterolateral attached with ceratobranchial 3, posteroventraly attached with caratobranchial 4 and posterodorsal attached with pharyngeal toothplate of the fourth epibranchial. Pharyngeal toothplate associated with epibranchial 4 and bearing two rows of six and four teeth on ventral surface.

Cranium. Mesethmoid located in anteriormost portion of neurocranium, slightly sloped and convex (Fig. 8); shaped as an equilateral triangle in dorsal view (Fig. 9); anteriorly articulate with frontals and ventrally connected to vomer. Vomer anteriorly expanded articulated with palatine, thin posteriorly, bearing one foramen on each side of anterior expansion.

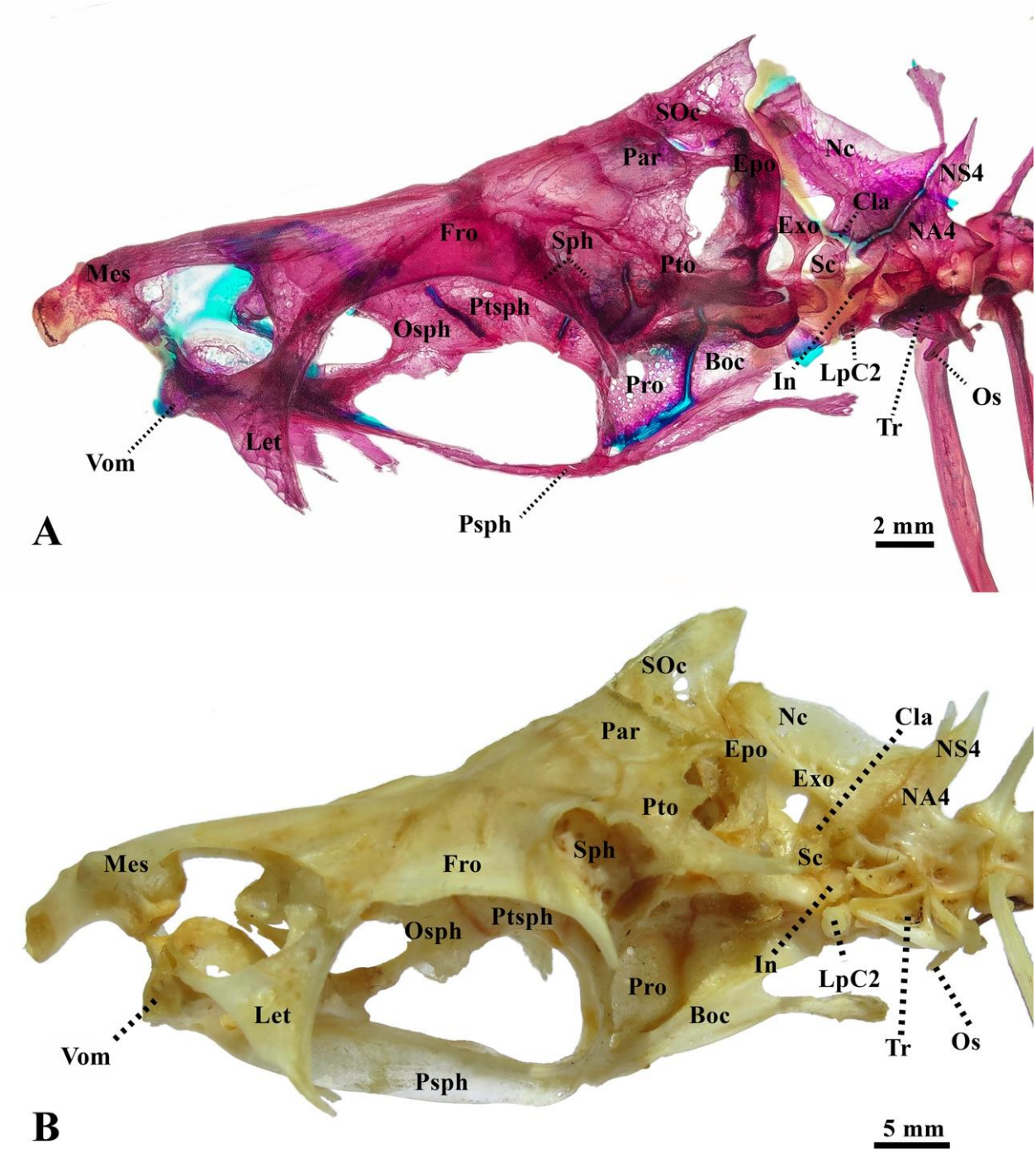
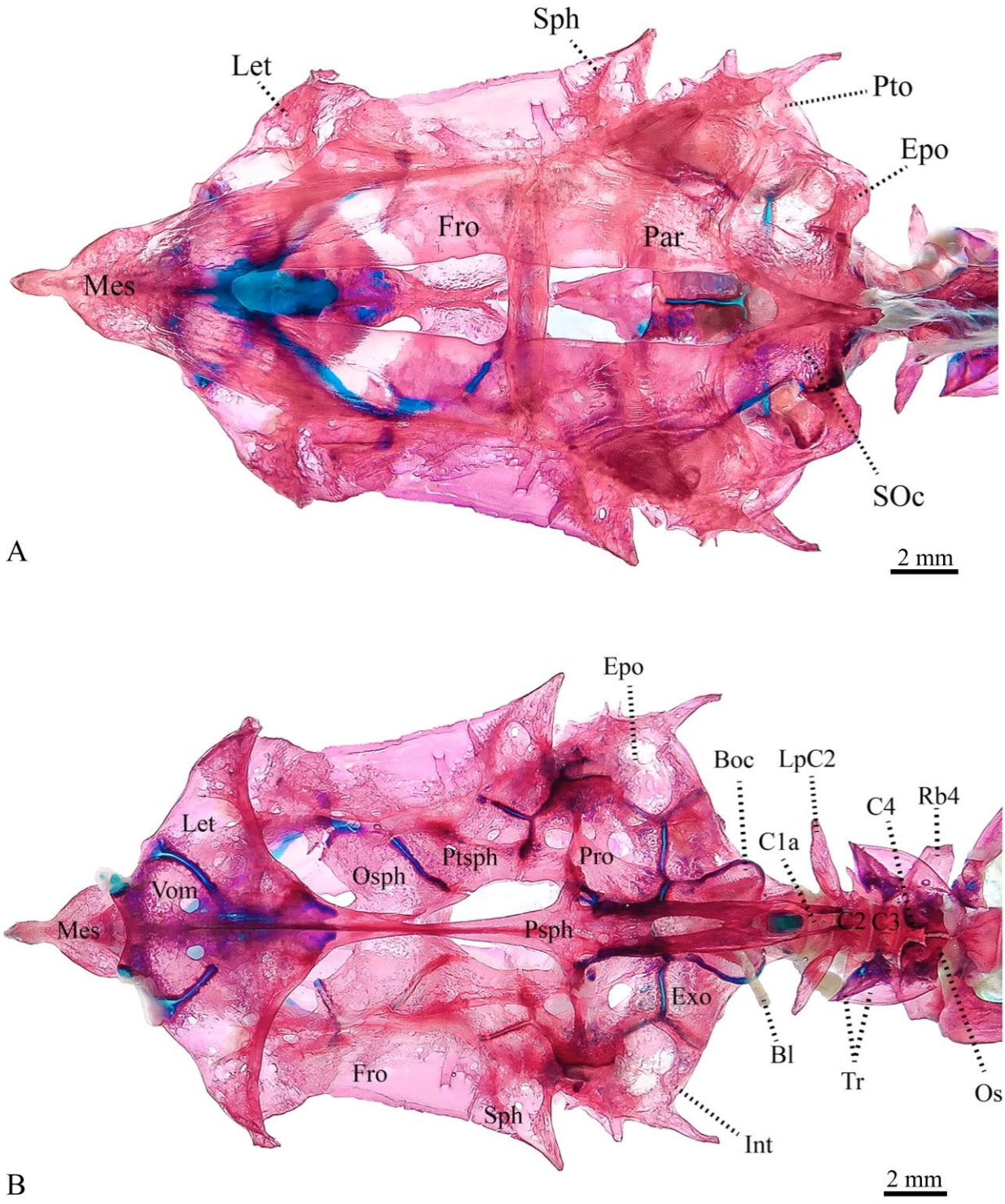


Figure 8. Cranium of "*Anostomoides*" *nattereri* lateral view (A and B), MZUSP 5429, 138.7 mm SL. **Bl:** baudelot ligament, **Boc**: basioccipital, **Cla:** *claustrum*, **Epo:** epioccipital, **Exo:** exoccipital, **Fro:** frontal, **In:** *intercalarium*, **Let:** lateral ethmoid, **LpC2:** lateral process of centrum2, **Mes:** mesethmoid, **NA4:** neural arch 4, **Nc:** neural complex, **NS4:**neural spine 4, **Os:** *os suspensorium*, **Osph**: orbitosphenoid, **Par:** parietal, **Pro**: prootic, **Pto**: pterotic, **Psph**: parasphenoid, **Ptsph**, pterosphenoid, **Sc:** *scaphium*, **SOc**: supraoccipital, **Sph**: sphenotic, **Tr**: *tripus*, **Vom:** vômer.

Lateral ethmoid large, with well-developed ventrolateral spine-like process, posterolateral margin forming orbit; anterodorsal margin forming floor of nasal cavity. Frontal large, forming most of dorsal surface of head, rectangular-shaped with more or less straight lateral margin, extended medially forming epiphyseal bar on centrum of fontanel. Parasphenoid long and thin, lateral process present at middle of bone, posteriorly extended under basioccipital and beyond forming paired irregular free process that is extended posteriorly till second vertebral centrum. Orbitosphenoid between sphenotic and frontal. Pterosphenoid laminar and thin, between orbitosphenoid, frontal, sphenotic and prootic. Sphenotic with ventrolateral spine-like process, anteroventral margin forming orbit. Prootic large, forming floor and sides of braincase, with three large foramina for trigemino-facial nerve trunk. Pterotic with well-developed posterolateral spine-like process.

Parietal nearly rectangular-shaped, dorsal, sutured to frontal, and separated from countersided part by cranial fontanel. Supraoccipital forming posterior margin of cranial fontanel and medial margin of posttemporal fossa, with acute posterior extension forming crest, the supraoccipital spine. Epioccipital trirradiated, forming margins of posttemporal and subtemporal fossae.



345

346 **Figure 9.** Cranium of "*Anostomoides*" *nattereri* in dorsal (A) and ventral view (A and B), MZUSP 5429,
347 138.7 mm SL. **Bl:** *baudelot* ligament, **Boc**: basioccipital, **C1-4:** *centrum* 1-4, **Cla:** *claustrum*, **Epo:**
348 epioccipital, **Exoc:** exoccipital, **Fro:** frontal, **In:** *intercalarium*, **Let:** lateral ethmoid, **LpC2:** lateral process
349 of *centrum* 2, **Mes:** mesethmoid, **NA4:** neural arch 4, **Nc:** neural complex, **NS4:**neural spine 4, **Os:** *os*
350 *suspensorium*, **Osph**: orbitosphenoid, **Par:** parietal, **Pro**: prootic, **Pto**: pterotic, **Psph**: parasphenoid, **Ptsph**,
351 pterosphenoid, **Rb4:** rib 4, **Sc:** *scaphium*, **SOc**: supraoccipital, **Sph**: sphenotic, **Tr**: *tripus*, **Vom:** vômer.

Basioccipital relatively small, ventrally covered by parasphenoid, expanded laterally forming part of lagenar capsule, and housing origin of *Baudelot* ligament; small cartilaginous portion on posteroventral margin. Intercalar small, *L*-shaped, attached mainly to prootic. Exoccipital large, forming most of posteroventral face of skull, bearing three foramina (lateral occipital foramen, magnum foramen, and vagus foramen).

Weberian apparatus. Neural complex large, laterally compressed with ventral margin slightly rounded, and bearing an invagination on anteroventral margin, attached to supraoccipital anteriorly, and posteriorly to basioccipital, neural arch of third vertebra and neural arch and spine of fourth vertebra (Fig. 8). *Scaphium* rounded, shell-shaped, with a small pinlike process ventrally articulated with first centrum. *Intercalarium* small, *L*-shaped, inserted on second vertebral centrum, posterodorsally articulate with neural arch of third vertebra, bearing a small anterolateral process (*manubrium intercalarii*) articulated with *scaphium*, and *tripus* by means of a strong fibrous ligament (Fig. 9). *Claustrum* small, blent, located between neural complex and *scaphium*. *Os supensorium* small, curved and directed medially, connected to counterpart medially by thin conective tissue. *Tripus* ventrally attached to third centrum, wide, mainly triangular, with thin hook-like projection posteromedially and passing through the fourth rib, anteriorlly, thin hook-like projection connected with *os supensorium* by connective tissue.

Vertebral centrum 1 shortest, bearing deep, narrow paired pits on dorsal margin articulated with ventral process of *scaphium*. Vertebral centrum 2 with anteroventral process extended anterolaterally. Vertebral centrum 3 large (compared to first and second centra), bearing a strong transverse process extended anterolaterally, and neural arch 3 with a small transverse process attached dorsally to neural complex. Fourth vertebral centrum larger than third, bearing broad neural arch and spine.

Six *T*-bone shaped supraneurals, inserted on dorsal midline of body between fourth to ninth vertebrae. First supraneural ventrally articulated with anterior margin of spine of fourth vertebra.

Pectoral girdle. Extrascapular small, ovoid, articulated with posttemporal and posterolateral region of cranium, bearing sensory canal with three pores, one directed to parietal, one to pterotic, and another to posttemporal (Fig. 10). Posttemporal laminar bearing two dorsally directed spine-like process, dorsally articulate with parietal, bearing sensory canal on ventral portion. Supracleithrum elongate, vertical, posterior margin concave, sensory canal present and exiting near medial portion towards body lateral line.

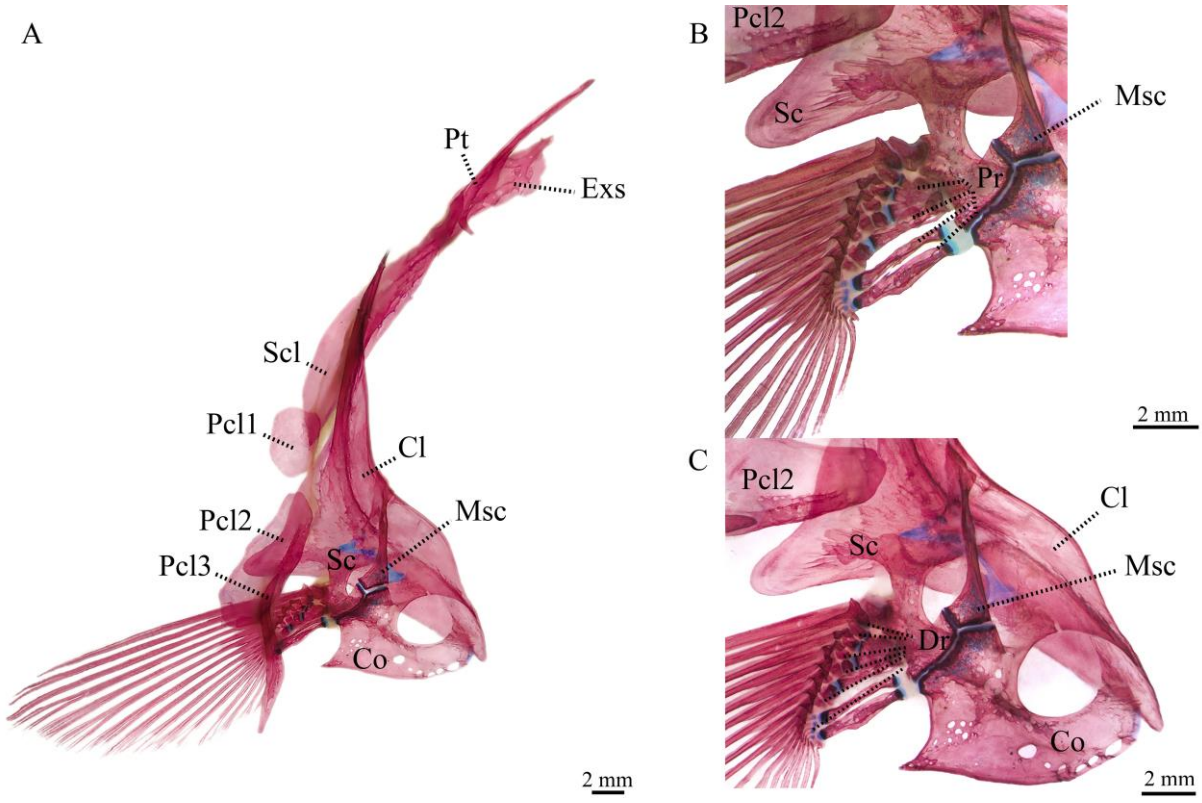
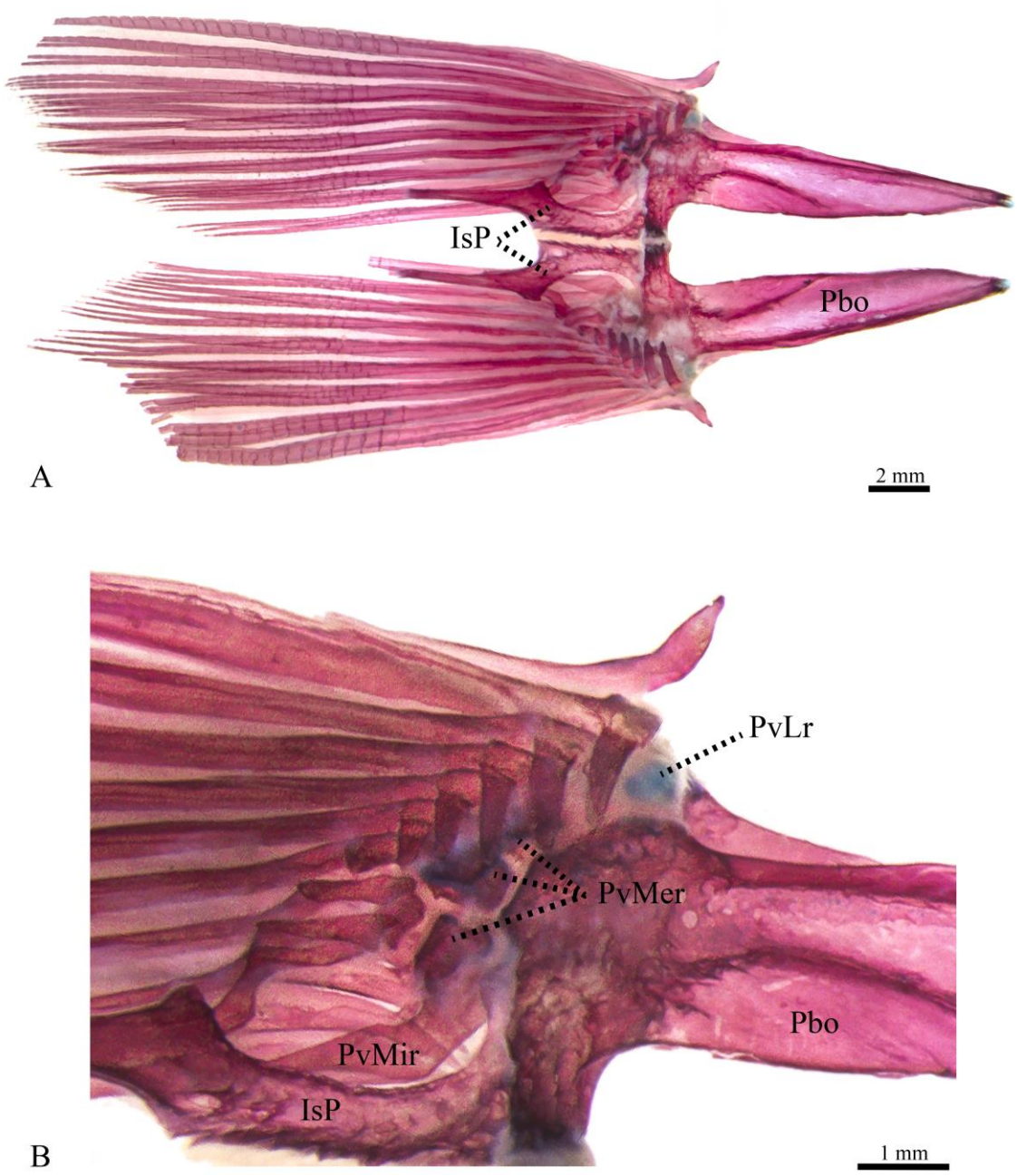


Figure 10. Pectoral fin of "*Anostomoides*" *nattereri*, MZUSP 5429, 138.7 mm SL. **Co:** coracoid, **Cl:** cleithrum, **Dt:** distal radial, Exs: extrascapular, **Msc:** mesocoracoid, **Pcl 1-3:** postcleithra 1-3, **Pr:** proximal radials, **Pt:** posttemporal, **Sc:** supracleithrum.

Cleithrum large, triangle-shaped, with dorsal process long tapering towards supracleithrum, folded medially on anterodorsal margin. Coracoid large, with two spine-like process, bearing a foramen on margin posterior. Mesocoracoid small, *J*-shaped, located between

393 coracoid and scapula. Scapula small, *I*-shaped, forming part of scapular foramen, with cleithrum.
394 Postcleithrum 1 small, ovoid, dorsal portion laterally overlapping supracleithrum. Postcleithrum 2
395 large, laterally overlapping cleithrum. Postcleithrum 3 elongated, rod-like and with sharp edges.
396 Series of pectoral radials composed by six proximal and eight distal elements. First three
397 proximals fused forming a single bone, other rod-ilke. First six distals ossified and lenticular, last
398 two small and cartilaginous. Pectoral fin with one unbranched and fifteen branched rays (Fig. 10).
399
400 **Pelvic girdle.** Pelvic bone strong, tapering anteriorly with cartilaginous tip (Fig. 11). Isquiatic
401 process strong, curved anteriorly, and sharp posteriorly. One pelvic-fin lateral radial, cartilaginous
402 and inserted on base of first and second pelvic-fin ray. Three pelvic-fin medial radials, ossified,
403 inserted between fourth and eightth pelvic-fin branched rays. One pelvic-fin middle radial,
404 ossified, similar and parallel to ischiatic process. Two unbranched and eight branched rays

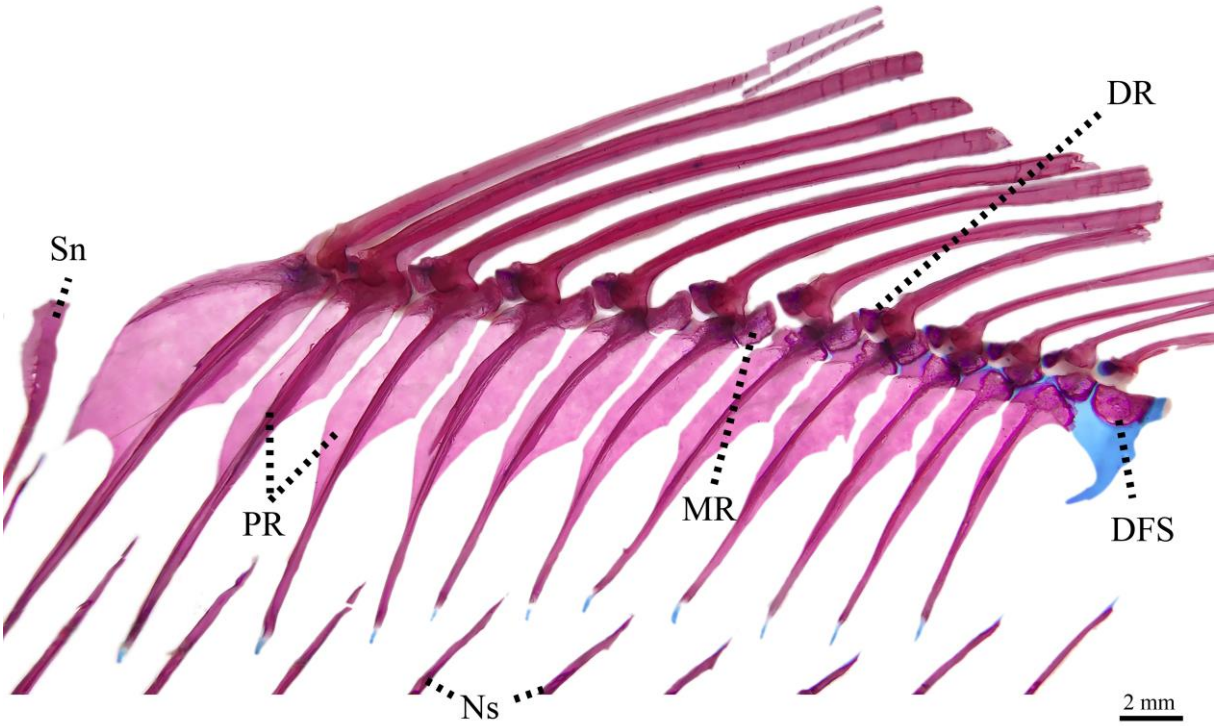


405

406 **Figure 11.** Pelvic fin of "*Anostomoides*" *nattereri*, MZUSP 5429, 138.7 mm SL. **IsP:** isquiatic process,
407 **PBo:** pelvic bone, **PvLr:** pelvic-fin lateral radial, **PvMer:** pelvic-fin medial radials, **PvMir:** pelvic-fin
408 middle radial
409

410 **Dorsal fin.** Dorsal fin with two unbranched and 10 branched rays (Fig. 12). First pterygiophore
411 large, inserted between neural spines of vertebrae 8 and 9, and supporting two dorsal-fin rays;
412 other 10 pterygiophores smaller and supporting one dorsal-fin ray each. Posterior to last proximal
413 pterygiophore, a hook shape piece cartilaginous (end piece, or dorsal fin stay). First dorsal-fin ray

414 articulated to first proximal radial, second to fifth rays articulated to proximal and distal radials,
415 and sixth to 13th ray articulate with medial and distal radials.



416

417 **Figure 12.** Dorsal fin of "*Anostomoides*" *nattereri*, MZUSP 5429, 138.7 mm SL. **DFS:** dorsal fin stay, **DR:**
418 distal radial, **MR:** medial radial, **Ns:** neural spine, **PR:** proximal radial, **Sn:** supraneural.
419

420 **Anal fin.** Anal fin with four unbranched rays and eigth branched rays (Fig. 13). First
421 pterygiophore large, inserted between neural spines of vertebrae 22 and 23 and supporting four
422 unbranched anal-fin rays; eight other pterygiophores smaller and supporting one branched anal-fin
423 ray each. First to fourth pterygiophores possessing only proximal and distal radials. Anal-fin
424 unbranched rays articulated with proximal and distal radials, fifth to 12th rays articulated with
425 medial and distal radials. An end piece (or anal-fin stay), posterior to last pterygiophore, hook
426 shape and cartilaginous.
427

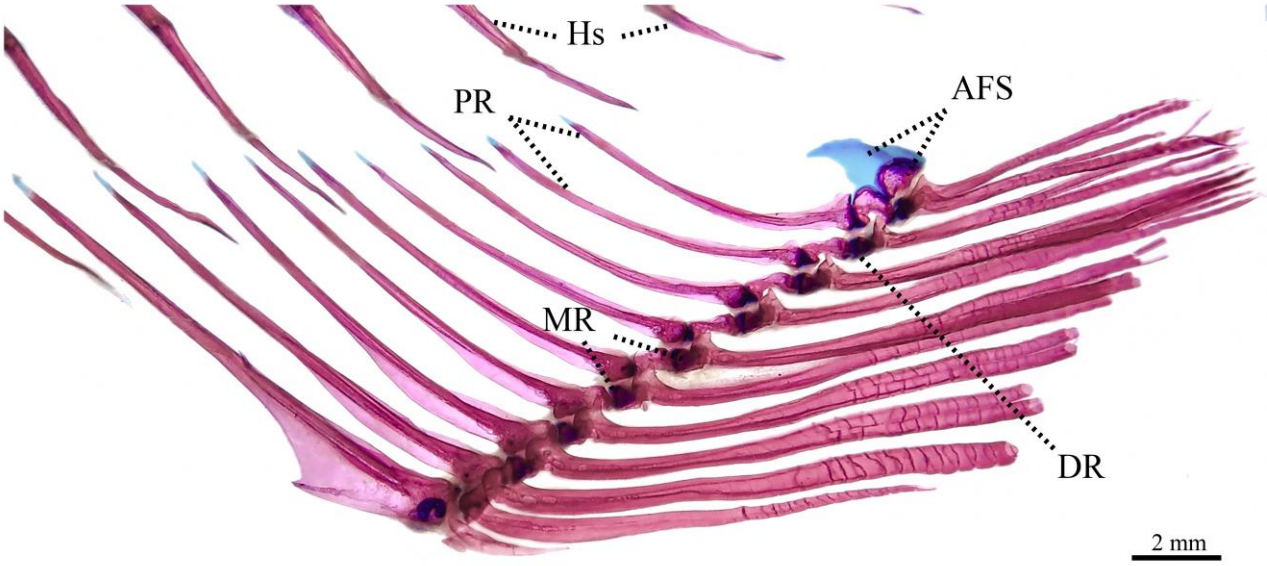


Figure 13. Anal fin of "*Anostomoides*" *nattereri*, MZUSP 5429, 138.7 mm SL. **AFS:** anal fin stay, **DR:** distal radial, **Hs:** haemal spine, **MR:** medial radial, **PR:** proximal radial.

Caudal skeleton. Caudal fin with six dorsal and five ventral procurrents rays, 10 principal caudal-fin rays on dorsal lobe and 9 on ventral lobe; base of lobes separated by diastema (Fig. 14). Rays on dorsal lobe supported by hypurals 4 to 6 and pleurostyle; rays on ventral lobe supported by parhypural, hypurals 1 and 2. Base of parhypural fused to compound centra (urostyle). Hypural 1 large, separeted from compound centra. Hypural 2 sutured to compound centra. Hypural 3 contacting compound centra. Hypural 4 to 6 gradually deacreasing in size posteriorly, separeted from compound centra. Opisthural cartilage *V*-shaped on posterior tip of notochord. Uroneural 1 large, closely attached to pleurostyle, uroneural 2 small, separate, located at distal tip of pleurostyle. Three epurals, first smallest, second longest. Neural and haemal spines of ural centra 2 and 3 plate-like, with spines of second centrum larger that those of third centrum. Cartilagenous stay anterior to first ventral procurrent ray.

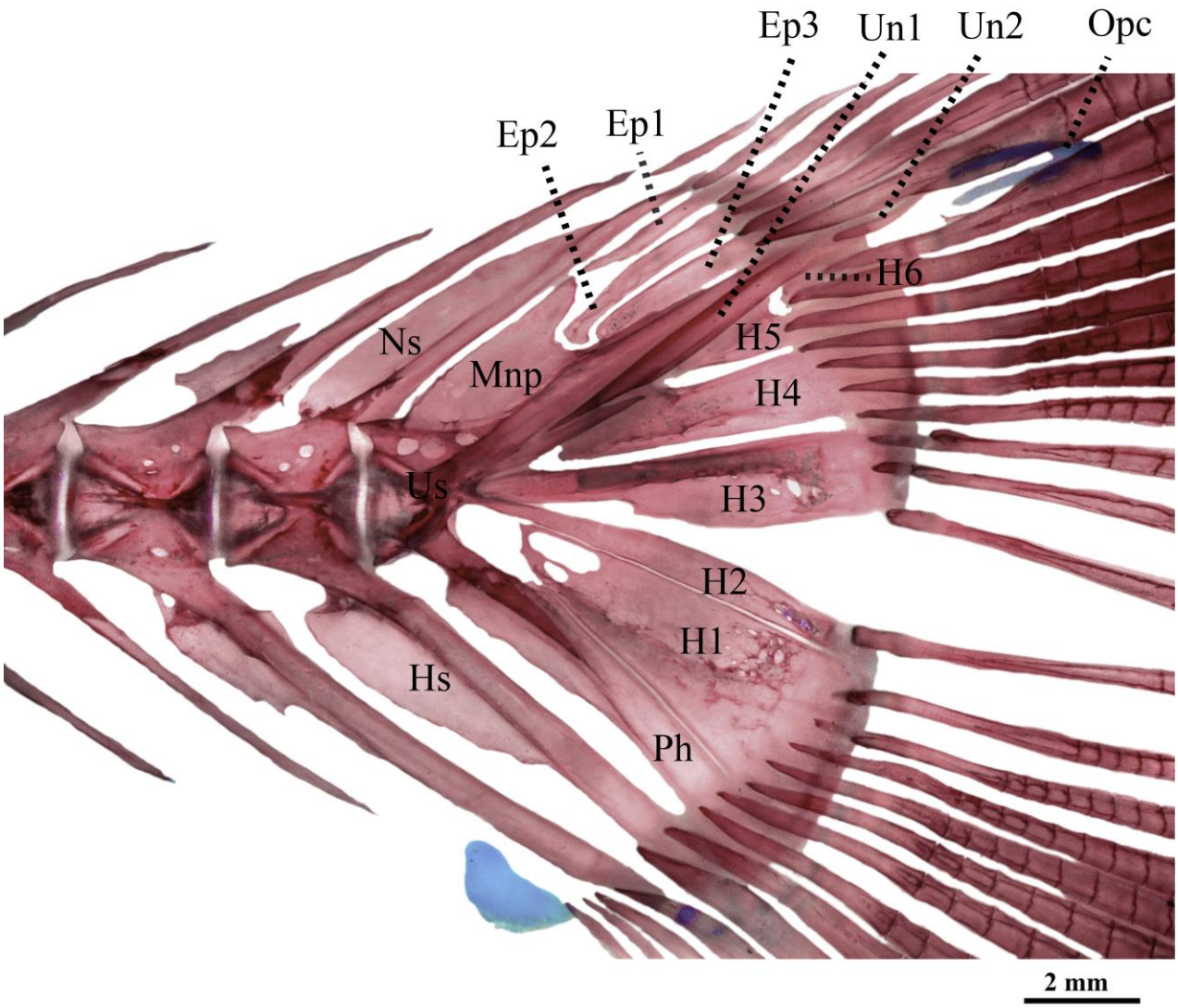


Figure 14. Caudal fin of "*Anostomoides*" *nattereri*, MZUSP 5429, 138.7 mm SL. **Ep 1-3:** epural 1-3; **H1-6:** hipurals 1-6; **Hs:** haemal spine; **Mnp:** modified neural process**, Ns:** neural spine, **Opc:** opisthural Cartilage, **Ph:** parhypural, **Un 1-2:** uroneural 1-2, **Us:** urostyle.

Etymology

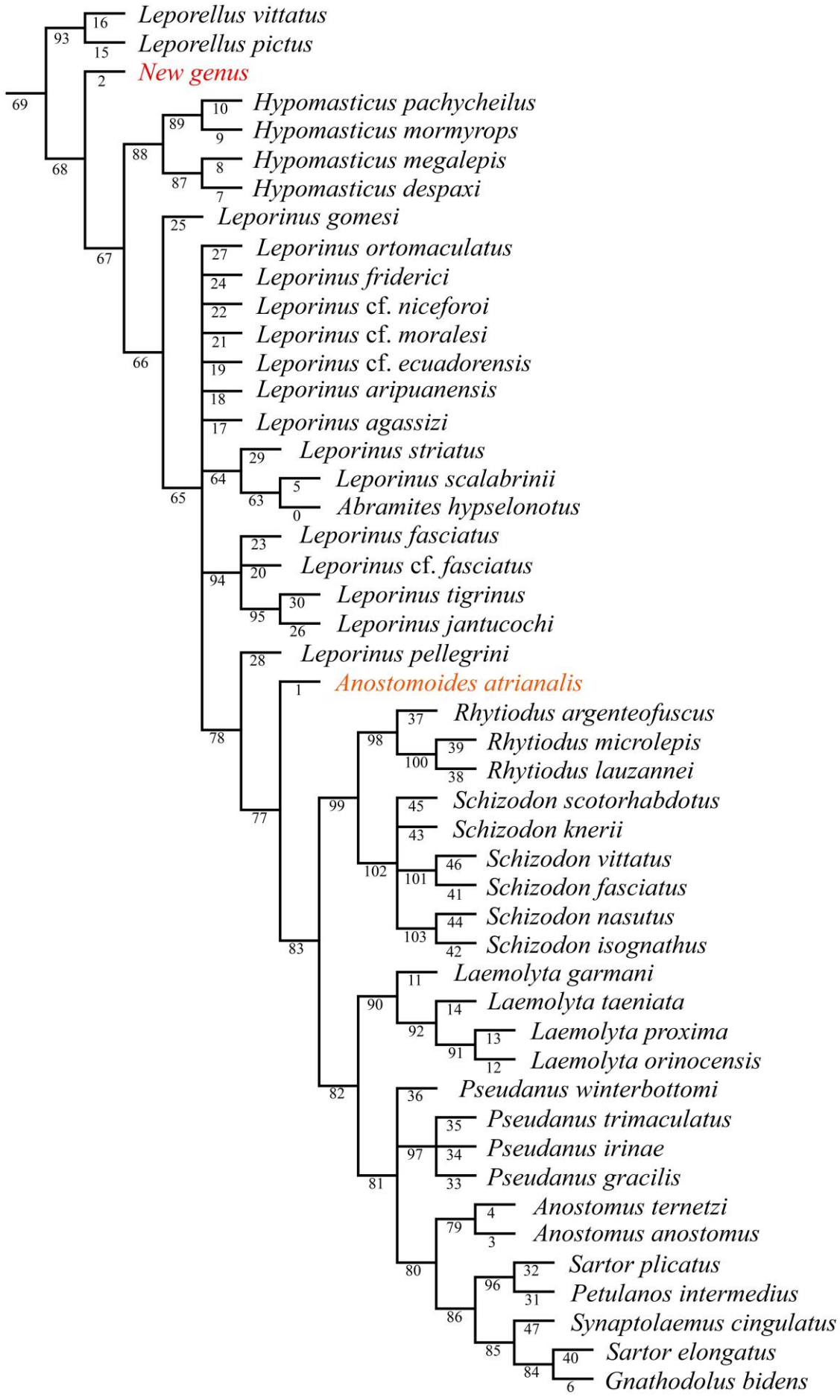
To be defined.

Phylogenetic relationships

The phylogenetic analysis based on 123 morphological characters coded for 48 ingroup taxa resulted in a total of 240 equally parsimonious trees with 523 steps each, consistency index equals to 0.390, and retention index equals to 0.800. The strict consensus tree (Fig. 15) shows that "*Anostomoides*" *nattereri* was recovered as sister to all anostomids, except for *Leporellus*,

whereas *Anostomoides atrianalis* was recovered as sister to Anostominae plus *Laemolyta*, *Rhytiodus*, and *Schizodon*.

The clade that included thte new genus close to all Anostomidae, except *Leporellus*, was supported by seven synapomorphies: 1) presence of ventromedial plate-like process of mesethmoid extended ventrally and posteriorly towards vomer: (Character 18: 0 > 1); 2) insertion of primordial ligament on medial surface of maxilla located within ventral half of longest axis of bone (Character 49: 0 > 1); 3) width of ventral portion of maxilla narrow, only slightly expanded in axis transverse to long axis of bone (Character 52: 1 > 0); 4) form of association of posterodorsal and posterior processes of quadrate separated with length of separate portion of posterodorsal process approximately twice width of process or greater (Character 76: 0 > 1); 5) symplectic long with posterior margin of bone situated proximate to ventral margin of hyomandibular (Character 87: 0 > 1); 6) one or two complete rows of teeth on tooth-plate of fifth ceratobranchial (Character 96: 2 > 1); and 7) presence of one or more dark blotch with distinct margins present along lateral-line scale row, each blotch approximately one to two scales in height (Character 118: 0 > 1).


Leporellus vittatus
Leporellus pictus
New genus
Hypomasticus pachycheilus
Hypomasticus mormyrops
Hypomasticus megalepis
Hypomasticus despaxi
Leporinus gomesi
Leporinus ortomaculatus
Leporinus friderici
Leporinus cf. niceforoi
Leporinus cf. moralesi
Leporinus cf. ecuadorensis
Leporinus aripuanensis
Leporinus agassizi
Leporinus striatus
Leporinus scalabrinii
Abramites hypselonotus
Leporinus fasciatus
Leporinus cf. fasciatus
Leporinus tigrinus
Leporinus jantucochi
Leporinus pellegrini
Anostomoides atrianalis
Rhytiodus argenteofuscus
Rhytiodus microlepis
Rhytiodus lauzannei
Schizodon scotorhabdotus
Schizodon knerii
Schizodon vittatus
Schizodon fasciatus
Schizodon nasutus
Schizodon isognathus
Laemolyta garmani
Laemolyta taeniata
Laemolyta proxima
Laemolyta orinocensis
Pseudanus winterbottomi
Pseudanus trimaculatus
Pseudanus irinae
Pseudanus gracilis
Anostomus ternetzi
Anostomus anostomus
Sartor plicatus
Petulanos intermedius
Synaptolaemus cingulatus
Sartor elongatus
Gnathodolus bidens

473

Figure 15. Strict consensus cladogram of 240 most parsimonious trees (540 steps, consistency index = 0.390, retention index = 0.800) constructed with 123 morphological data, showing the inter-relationships amongst of the "*Anostomoides*" *nattereri* and the remainder Anostomidae.

The clade that included all Anostomidae, except *Leporellus* and "*Anostoimoides*" *nattereri*, was recovered and supported by four synapomorphies: 1) anteroventral portion of sixth infraorbital not greatly expanded and overlapping anteroventral process of sphenotic (Character 13: 0 > 1); 2) two cusps on second and third teeth of premaxilla (Character 33: 1 > 2); 3) palatine with distinct plate- or finger-like process extending away from main, rounded portion of bone cradled by dorsal portion of ectopterygoid (Character 67: 0 > 1); and 4) process of palatine with distinct lateral, anterolateral or anteroventral orientation (Character 68: 0 > 1).

The five synapomorphies that was recovered and supported the clade that included the genera *Anostomoides*, *Laemolyta*, *Schizodon*, *Rhytiodus* plus subfamily Anostominae was: 1) retroarticular ventrally situated in lower jaw and forms part of ventral margin of lower jaw, line drawn along ventral margin of retroarticular barely, if at all, intersects ventral portion of dentary (Character 65: 0 > 1); 2) posterodorsal margin of opercle continuously convex or straight and completely lacking concavity (Character 90: 0 > 1); 3) presence of ossified first basibranchial (Character 92: 1 > 0); 4) presence of supraneural dorsal to Weberian apparatus (Character 106: 1 > 0); 5) presence of complete dark stripe along lateral-line scale row (Character 120: 0 > 1).

The new genus possesses nine non-exclusive autapomorphies: 1) flange of fifth infraorbital posterior of sensory canal, less extensive or entirely absent, with at least dorsal section of flange missing (Character 11: 0 > 1); 2) presence of deep grooves on each side of vomer that receive dorsal portion of entopterygoid and metapterygoid (Character 20: 0 > 1); 3) presence of at least two teeth on premaxilla with strong ventral bend followed by anterior-facing alignment, resulting in zigzag shape to tooth in lateral profile (Character 35: 0 > 1); 4) presence of distinct notch in posterior lamina of symphyseal tooth of dentary (Character 39: 0 > 1); 5) main body of symphyseal tooth of dentary with straight incisiform margin and no apparent cusps (Character 41: 1 > 0); 6) main body of third tooth of dentary with two distinct cusps (Character 43: 1 > 2); 7)

presence of dermal papillae on lower lip: (Character 66: 0 > 1); 8) length of process of palatine very long, length of process approximately two or more times width of process (Character 69: 0 > 1); and 9) one or two full rows of teeth on fifth upper pharyngeal tooth-plate (Character 94: 2 > 1).

The phylogenetic analysis based on molecular data recovered "*Anostomoides*" *nattereri* as sister group to all anostomids (Fig. 16). Even though the supports of the lowermost branches are relatively low, this new hypothesis corroborates the polyphyly of *Anostomoides* (as previous defined, Santos & Zuanon, 2006; Assega & Birindelli, 2019) and the need to recognize a new genus to allocate "*Anostomoides*" *nattereri*, confirming the results based on morphology.

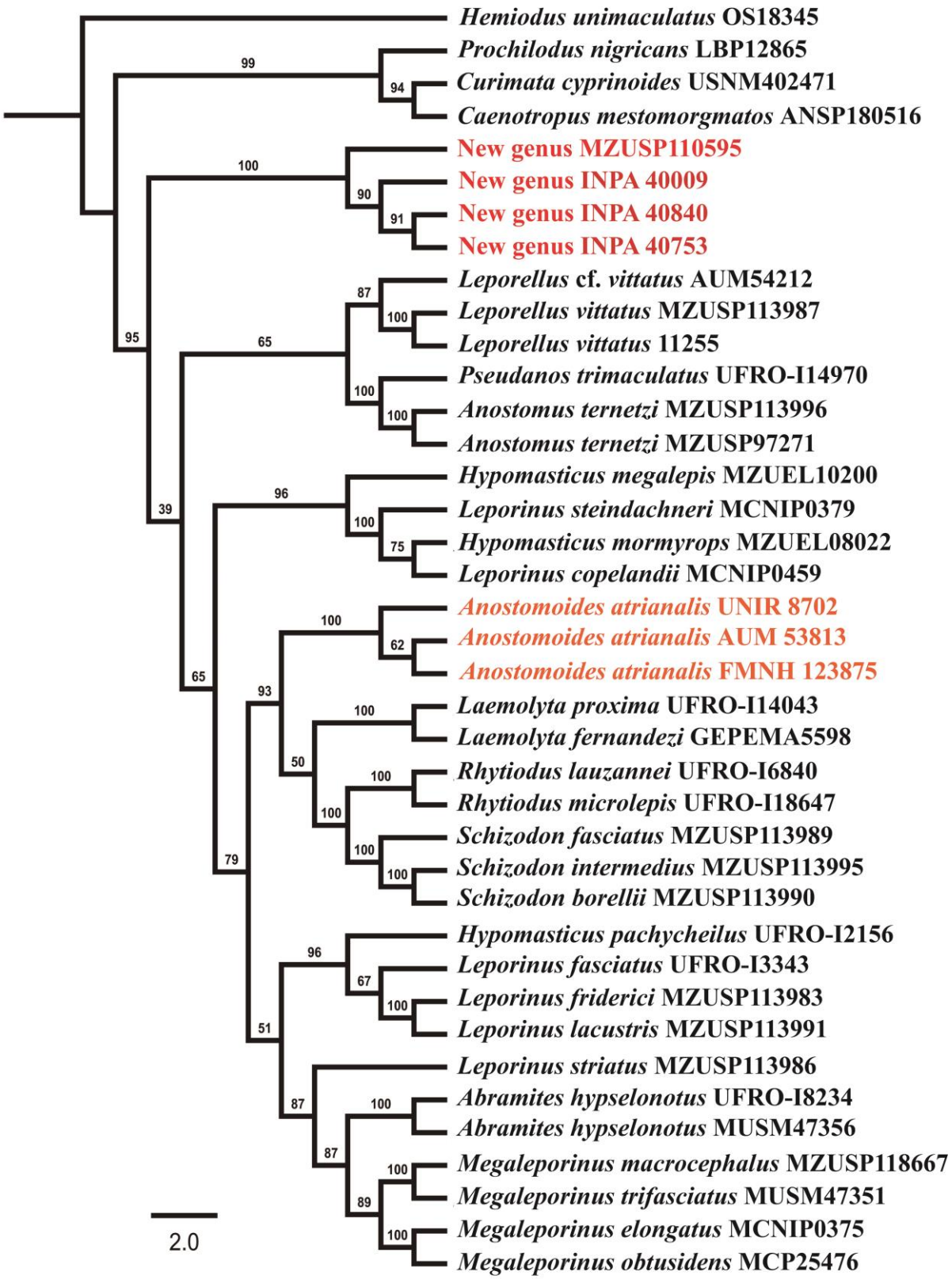


Figure 16. Phylogenetic tree showing relationships among the species of Anostomidae analyzed by a Maximum Likelihood (ML) resulted from five genes sequences. The numbers on the nodes are bootstrap support.

DISCUSSION

Assega & Birindelli (2019) diagnosed *Anostomoides* using a combination of non-exclusive characters, including mouth upturned or slightly upturned with four teeth on premaxillary, including symphyseal tooth unicuspid or bicuspid, remaining teeth slightly tricuspid (with medial cuspid distinctly larger); four dentary teeth, symphyseal tooth with truncate cutting edge (without cusps); and second tooth with a single large cusp, and two lateral teeth with small cusps (three or slightly more cusps). Nevertheless, all these characters are homoplastic and present in distinct genera of Anostomidae. In addition, *Anostomoides atrianalis* shares with *Abramites*, *Laemolyta*, *Leporinus*, *Megaleporinus*, *Rhytiodus*, and *Schizodon* several morphological characters, and strongly supported relationship based on molecular data. These characters and the molecular support are not shared by "*Anostomoides*" *nattereri*, leaving no doubt of the polyphyly of the former *Anostomoides* (as defined in previous studies), prompting the need of the recognition of a new genus to allocate "*Anostomoides*" *nattereri*.

Based on the results obtained independently using morphological and molecular characters, "*Anostomoides*" *nattereri* occupies a relatively basal position among Anostomidae, as sister group to all remaining genera (Fig. 16), or alternatively to all except *Leporellus* (Fig. 15). The most interesting feature that is responsible for recovering the new genus close to *Leporellus* (at the base of the Anostomidae) is the absence of a lateroanterior directed process on the palatine. The condition present in the new genus is very similar to that present in the Anostominae, and very distinct from the condition present in other Anostomidae, including *Leporinus* and *Anostomoides atrianalis* (Figs. 2–3). Interestingly, *Leporellus* has an intermediate condition (compared to the new genus and derived anostomids such as *Leporinus*), in which the process is present but not blent anterolaterally (Fig. 3). Sidlauskas & Vari (2008) considered the palatine to be modified in other families of Anostomoidea and did not code these taxa for characters 67 and 68. Nevertheless, the palatine of Chilodontidae, Curimatidae, and Prochilodontidae (Fig. 2) is

similar to the condition present in the new genus and Anostomidae, in which the palatine is bean-shaped and lack any distinct process. Therefore, it is likely that the presence of a lateroanteriorly directed process on the palatine is a synapomorphy for the Anostomidae (except the new genus, and *Leporellus*).

Another interesting feature that is diagnostic for the new genus is the presence of dermal papillae on the upper and lower lips (Fig. 3). Even though this feature was considered as eclusive to *Sartor*, *Synaptolaemus* and *Gnathodolus* by Winterbottom (1980) and Sidlauskas & Vari (2008: character 66), dermal papillae is conspicuously present in the upper and lower lips of all Anostominae, as showed by Birindelli, Lima & Britski (2012) for *Pseudanos*. The presence of shared characters between the new genus, *Leporellus* and the Anostominae indicate an alternative scenario in which these three groups are at the base of the Anostomidae. Interestingly, this scenario corroborates, in part, the phylogenetic hypothesis based on the molecular data, in which the Anostominae has a more basal position, and could represent the best explanation to solve the conflit in the results obtained in the two independent analyses.

On the other hand, the relationship between *Anostomoides atrianalis*, *Laemolyta*, *Rhytiodus*, and *Schizodon* were recovered based on morphological and molecular data in the present study as well as in previous studies (Sidlauskas & Vari, 2008; Ramirez, Birindelli & Galetti, 2016a; Ramirez, Carvalho-Costa, Venere, Carvalho, Troy & Galetti (2016b). Several morphological characters support this relationship, including: 1) retroarticular ventrally situated in lower jaw and forming part of ventral margin of lower jaw, line drawn along ventral margin of retroarticular barely, if at all, intersects ventral portion of dentary (Character 65, State 1); 2) posterodorsal margin of opercle showing continuously convex or straight and completely lacking concavity (Character 90, State 1); 3) first basibranchial cartilaginous (Character 92, State 0); 4) Weberian apparatus lacking a dorsal supraneural (Character106, State 0); 5) presence of complete dark stripe along lateral-line scale row (Character 120, State 1).

566 Four characters were coded distinctly for *Anostomoides atrianalis* in the present study, in
567 comparison to Sidlauskas & Vari (2008). Character 13 was coded as 0 instead of as 1 because in
568 the examined specimens anteroventral portion of sixth infraorbital expanded and overlapping
569 anteroventral process of sphenotic, with anterior margin of sixth infraorbital reaching or
570 surpassing anterior border of ventral process of sphenotic that forms posterodorsal portion of the
571 bony orbit. . Character 38 was coded as polymorphic by Sidlauskas & Vari (2008), but was coded
572 as 0 in the present study, as all examined specimens showed dentary teeth with large, well-
573 developed posterior lamina.. Character 44 was coded as missing data by Sidlauskas & Vari
574 (2008), however, we coded it as "posterior lobes of dentary teeth absent, or if posterior lobes
575 present, no distinct cusp present on posterior lobes of toot". In the character 118, Sidlauskas &
576 Vari (2008) did not observed lateral-line spots (State 0), however, we observed "series of one or
577 more dark spots with distinct margins present along lateral-line scale row, each spot
578 approximately one to two scales in height" (State 1). The distinct interpretations are possibly due
579 to the small number and small size of specimens used by Sidlauskas & Vari (2008). Nevertheless,
580 these differences did not alter the results nor the strong support for considering *Anostomoides*
581 *atrianalis* as closely related to *Laemolyta*, *Rhytidous*, and *Schizodon*.
582
583 **Comparative material**
584 **Morphological analysis**
585 For a complete list of specimens of *Anostomoides atrianalis* and "*Anostomoides*" *nattereri* see
586 Assega & Birindelli (in press). *Abramites hypselonotus*: MZUSP 48123, 1 C&S, 63.5 mm SL,
587 Amazonas, Coari, Rio Solimões, Ilha Sorubim (03º55'00" S, 63º20'00" W), Expedição
588 Permanente à Amazônia, 29 September 1968. *Anostomoides atrianalis* ANSP 159599, 1 C&S,
589 159.6 mm SL, Bolivar, Cano (possibly Cano Curimo) feeding río Caura near confluence with río
590 Caura and río Orinoco (07°37'48" N, 64°50'42" W), B. Chernoff, W. Saul & R. Royero, 22

November 1985. *Anostomus anostomus*: MZUSP 85153, 2 C&S, 89.5 to 90.4 mm SL, Amazonas, Rio Tiquié, abaixo da cachoeira do Caruru (00º16'28,9" N, 69º54'53,4" W), F.C.T. Lima, 30 June 2004. *Caenotropus labyrinthicus*: MZUSP 29351, 1 C&S, 68.9 mm SL, Roraima, Ilha Cantagalo, Rio Branco (01º30'00" N, 61º16'00" W), M. Goulding, 28 October 1979. *Laemolyta fernandezi*: MZUSP 91837, 1 C&S, 94.0 mm SL, Mato Grosso, Paranatinga, Córrego na Fazenda Lício, tributary of Rio Culuene (13º50'22" S, 53º14'59" W), J.L.O. Birindelli, L.M. Sousa river & A. Akama, 21 August 2008. *Laemolyta proximai*: MZUSP 22105, 1 C&S, 109.0 mm SL, Pará, São Luís, Rio Tapajós, Ilha da Barreirinha (04º27'00" S, 56º15'00" W), Expedição Permanente à Amazônia, 21 November 1970. *Leporellus vittatus*: MZUSP 106332, 1 Sk, 155.0 mm SL, São Paulo, Descalvado, Ribeirão do Pântano, at the confluence of the Rio Mogi Guaçú (21º56'00" S, 47º34'00" W), P.H. Carvalho, 20 June 2009. *Leporinus obtusidesn:* MZUEL 16470, 1(Sk), 260.0 mm SL, Minas Gerais, Buritizeiro, Rio São Francisco, J.L.O. Birindelli, F.C. Jerep, E. Santana & R.H.C. Nascimento, 07 July 2016. *Prochilodus nigricans*: MZUSP 95799, 1 C&S, 112.5 mm SL, Mato Grosso, Itaúba, stream the edge of the dirt road, a tributary of rio Tele Pires (11º42.0' S, 55º35'21" W), J.L.O. Birindelli & P.H. Carvalho, 30 September 2007. *Prochilodus vimboides*: MZUEL 17834, 1 Sk, 189.1 mm SL, Minas Gerais, Águas Vermelhas, Estação de Piscicultura UHE Machado Mineiro (15º31'16.3" S, 41º30'14.8" W), J.L.O. Birindelli, F.C. Jerep, E. Santana & R.H.C. Nascimento, 03 July 2016. *Petulanos intermedius*: MZUSP 97330, 1 C&S, 59.6 mm SL, Pará, Novo Progresso, Rio Jamanxim river, near the Village Mil (07º43'51" S, 55º16'36" W), J.L.O. Birindelli, L. Sousa. A.N. Ferreira, M. Sabaj & N. Lujan, 23 October 2007. Pseudanos *irinae*: MZUSP 101646, 1 C&S, 92.9 mm SL, Amapá, Laranjal do Jari, left bank of the Rio Jari, upstream of Santo Antônio waterfall and upstream of the Rio Iratapuru (00º34'16" S, 52º34'44" W), J.L.O. Birindelli & P.H. Carvalho, 13 September 2008. *Pseudanos trimaculatus*: MZUSP 103509, 1 C&S, 105.7 mm SL, Amapá, Laranjal do Jari, Igapó on the left bank of the Rio Jari, upstream of Santo Antônio waterfall and upstream of the Rio Iratapuru (00º35'05" S, 52º36'59"

W), J.L.O. Birindelli, L. Sousa & M. Soares, 22 February 2009. *Rhytiodus microlepis*: INPA 16180, 1 C&S, 99.7 mm SL, Amazonas, Rio Solimões, ilha da Marchantaria, J. Cidoca, 01 October 1979. *Sartor respectus*: MZUSP 94867, 1 C&S, 80.9 mm SL, Mato Grosso, Paranatinga, Rio Culuene, drained stretch for the construction of the Paranatinga 2 (13º49'00" S, 53º15'00" W), L. Sousa. A.N. Ferreira, C.A. Machado & F. Machado, 02 July 2007.

Acknowledgments

We would like to thank Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) by fellowship grant, to Programa de Pós-Graduação em Ciências Biológicas of Universidade Estadual de Londrina. O.A. Shibatta and F. Jerep (UEL), F.O. Martins (IFPR-Londrina), J.C. Garavello (UFSCAR), G.S.C. Silva (UNESP-Botucatu), and C. Moreira (UFRJ) for discussions and valious suggestions to the present study. For loans and exchanges of specimens we thank: A. Datovo (MZUSP), C.S. Pavanelli (NUPÉLIA-UEM), H. Ortega (MUSM), L. Rapp Py-Daniel (INPA), L. Sousa (LIA), M.R.M. Fernandes (UFRO-ICT), M. Sabaj (ANSP), J. Armbruster and D. Werneke (AUM), M. Britto (MNRJ), and W.B. Wosiacki (MPEG). We thank A. Datovo (MZUSP), C. Ribas (INPA), M. Sabaj (ANSP – Projeto iXingu), T. Hrbek and I. Farias (UFAM – Projeto CNPq/SISBIOTA – BioPHAM) for loan of tissues and voucher. We thanks A. Datovo, M.D. Gianeti and O. Oyakawa (MZUSP), C. Oliveira (UNESP- Botucatu) and L. Rapp Py-Daniel (INPA) for as assistances during collections visits.

Literature Cited

Abe, K.T., Mariguela, T.C., Avelino, G.S., Castro, R.M.C. & Oliveira, C. (2013). Multilocus molecular phylogeny of Gasteropelecidae (Ostariophysi: Characiformes) reveals the existence of an unsuspected diversity. *Molecular Biology and Evolution*, *69,* 1209–14. https://doi.org/10.1016/j.ympev.2013.07.005

641 Assega, F.M. & Birindelli, J.L.O. (2019) Taxonomic revision of the genus *Anostomoides*
642 (Characiformes: Anostomidae). *Zootaxa*, 4646(1), 124–144.
643 Arratia, G. (1992). Development and variation of the suspensorium of primitive catfishes
644 (Teleostei: Ostariophysi) and their phylogenetic relationships. *Bonner Zoologische*
645 *Monographien*, *32*, 1–149.
646 Bemis, W.E., Hilton, E.J., Brown, B., Arrindell, R., Richmond, A.M., Little, C.D., Grande, L., ...
647 Nelson, G.J. (2004). Methods for preparing dry, partially articulated skeletons of
648 Osteichthyans, with notes on making Ridewood dissections of the cranial skeleton. *Copeia,,*
649 *2004*(3), 603–609.
650 Birindelli, J.L.O., Lima, F.C.T. & Britski, H.A. (2012). New species of *Pseudanos* Winterbottom,
651 1980 (Characiformes: Anostomidae) with notes on the taxonomy of *P. gracilis* and *P.*
652 *trimaculatus*. *Zootaxa, 3425*, 55–68.
653 Bogan, S., Sidlauskas, B., Vari, R.P. & Agnolin, F. (2012). *Arrhinolemur scalabrinii* Ameghino,
654 1898, of the late Miocene – a taxonomic journey from the Mammalia to the Anostomidae
655 (Ostariophysi: Characiformes). *Neotropical Ichthyology*, *10*, 555–560.
656 Borodin, N.A. (1931). On the genus *Anostomus* (Family Characinidae). *Bulletin of the Museum of*
657 *Comparative Zoology*, *72*, 37–52.
658 Edgar, R. C. (2004). MUSCLE: a multiple sequence alignment method with reduced time and
659 space complexity. *BMC bioinformatics*, *5*(1), 113. https://doi.org/10.1186/1471-2105-5-113.
660 Eigenmann, C.H. (1912) The freshwater fishes of British Guiana, including a study of the
661 ecological grouping of species, and the relation of the fauna of the plateau to that of the
662 lowlands. *Memoirs of the Carnegie Museum*, *5* (1), i–xxii + 1–578, pls. 1–103.
663 Garavello, J.C. & Britski, H.A. (2003) Family Anostomidae. 71–84. *In:* Reis, R.E., S.O. Kullander
664 & C.J. Ferraris (Eds.), *Check list of the freshwater fishes of South and Central America.*
665 *Edipucrs, Porto Alegre*.

666 Géry, J. (1974). Notes sur quelques Anostomidae (Pisces, Characoidei) du bassin Amazonien. *Vie*
667 *Milieu 1972-193*, *23,* 143–175.
668 Goloboff, P. A., Farris, J. S. & Nixon, K. C. (2008). TNT, a free program for phylogenetic
669 analysis. Cladistics, 24, 774–786.
670 Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., ...
671 Drummond, A., (2012). Geneious Basic: an integrated and extendable desktop software
672 platform for the organization and analysis of sequence data. *Bioinformatics*, *28*, 1647–1649.
673 https://doi.org/10.1093/bioinformatics/bts199
674 Li, C., Ortí, G., Zhang, G., & Lu, G. (2007). A practical approach to phylogenomics: The
675 phylogeny of ray-finned fish (Actinopterygii) as a case study. *BMC Evolutionary Biology, 7*,
676 44.
677 Lovejoy, N.R. & Collette, B.B. (2001). Phylogenetic Relationships of New World Needlefishes
678 (Teleostei: Belonidae) and the Biogeography of Transitions between Marine and Freshwater
679 Habitats. *Copeia, 2001*(2001), 324–338.
680 Maddison, W. P., & Maddison, D. R. (2017). Mesquite: A modular system for evolutionary
681 analysis. Version 3.2. Retrieved from http:// mesquiteproject.org
682 Mattox, G.M., Britz, R., & Toledo-Piza, M. (2016). Osteology of *Priocharax* and remarkable
683 developmental truncation in a miniature Amazonian fish (Teleostei: Characiformes:
684 Characidae). *Journal of morphology, 277*(1), 65–85.
685 Melo, B.F., Benine, R.C., Mariguela, T.C. & Oliveira, C. (2011). A new species of
686 *Tetragonopterus* Cuvier, 1816 (Characiformes: Characidae: Tetragonopterinae) from the rio
687 Jari, Amapá, northern Brazil. *Neotropical Ichthyology, 9*, 49–56.
688 https://doi.org/10.1590/S1679-62252011000100002

689 Melo, B.F. (2015) Relações filogenéticas na superfamília Anostomoidea (Ostariophysi:
690 Characiformes). Universidade Estadual Paulista Júlio de Mesquita Filho, Instituto de
691 Biociências de Botucatu, Botucatu, 181 pp.
692 Myers, G.S. (1950). Studies on South American fresh-water fishes. II. The genera of Anostomine
693 characids. *Stanford Ichthyological Bulletin, 3*, 185–197.
694 Nelson, J.S., Grande, T. & Wilson, M.V.H. (2016). Fishes of the World. 5th ed. Hoboken (NJ), J.
695 Wiley & Sons.
696 Palumbi, S. R. (1996). Nucleic acids II: The polymerase chain reaction. In D. M. Hillis, C. Moritz,
697 & B. K. Mable (Eds.), *Molecular systematics* (2nd ed., pp. 205–247). Sunderland, MA:
698 Sinauer.
699 Pellegrin, J. (1909) Characinidés américains nouveaux de la collection du Muséum d'Histoire
700 Naturelle. *Bulletin du Muséum National d'Histoire Naturelle, 14*(7), 342–347.
701 Ramirez, J.L. (2015) Filogenia molecular dos Anostomidae e filogeografia das espécies com
702 cromossomos sexuais ZZ/ZW do gênero *Leporinus*. Universidade Federal de São Carlos,
703 Centro de Ciências Biológicas e da Saúde, São Carlos, 150 pp.
704 Ramirez, J.L., Birindelli, J.L.O. & Galetti, P.M. (2016a) A New Genus of Anostomidae
705 (Ostariophysi: Characiformes): Diversity, Phylogeny and Biogeography Based on
706 Cytogenetic, Molecular and Morphological Data. *Molecular Phylogenetics and Evolution*,
707 *107*, 308–323.
708 Ramirez, J.L., Carvalho-Costa, L.F., Venere, P.C., Carvalho, D.C., Troy, W.P., Galetti, P.M.
709 (2016b). Testing monophyly of the freshwater fish *Leporinus* (Characiformes, Anostomidae)
710 through molecular analysis. *Journal Fish Biology*, *88*, 1204–1214.
711 Ramirez, J.L., Birindelli, J.L.O., Carvalho, D.C., Affonso, P.A.M., Venere, P.C., Ortega, H.,
712 Carrillo-Avila, … Galetti, P.M. (2017) Revealing Hidden Diversity of the Underestimated

713 Neotropical Ichthyofauna: DNA Barcoding in the Recently Described Genus *Megaleporinus*
714 (Characiformes: Anostomidae). *Frontiers in Genetics*, *8*, 149.
715 Sabaj, M. H. (Ed.) (2016). Standard symbolic codes for institutional resource collections in
716 herpetology and ichthyology: An online reference. Version 6.5 Retrieved from
717 http://www.asih.org
718 Santos, G.M. & Zuanon, J.A.S. (2006) *Anostomoides passionis*, a new fish species from Rio
719 Xingu, Brasil (Characiformes: Anostomidae). *Zootaxa, 1168,* 59–68.
720 Sidlauskas B. & Vari R.P. (2008). - Phylogenetic relationships within the South American fish
721 family Anostomidae (Teleostei, Ostariophysi, Characiformes). *Zoological Journal of the*
722 *Linnean Society. 154*, 70–210. DOI: 10.1111/j.1096-3642.2008.00407.x.
723 Stamatakis, A. (2006). RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with
724 thousands of taxa and mixed models. *Bioinformatics, 22*, 2688–2690.
725 https://doi.org/10.1093/bioinformatics/ btl446
726 Stamatakis, A., Hoover, P., & Rougemont, J. (2008). A rapid bootstrap algorithm for the RAxML
727 web servers. *Systematic Biology, 57*, 758–771.
728 Taylor, W.R. & Van Dyke, G.C. (1985). Revised procedures for staining and clearing small fishes
729 and other vertebrates for bone and cartilage study. *Cybium, 9*, 107–119.
730 Vari, R.P. (1983). Phylogenetic relationships of the Families Curimatidae, Prochilodontidae,
731 Anostomidae, and Chilodontidae (Pisces, Characiformes). *Smithsonian Contributions to*
732 *Zoology*, *378*, 1–60.
733 Weitzman, S.H. (1962). The osteology of *Brycon meeki*, a generalized characid fish, with an
734 osteological definition of the family. *Stanford Ichthyogical Bulletin, 8*, 3-77.
735 Weitzman, S.H. (1974). Osteology and evolutionary relationships of the Sternoptychidae, with a
736 new classification of stomiatoid families. *Bulletin of the American Museum of Natural*
737 *History, 153*, 327-478.

738 Winterbottom R (1980) Systematics, osteology and phylogenetic relationships of fishes of the
739 ostariophysan subfamily Anostominae (Characoidei, Anostomidae). *Life Sciences*
740 *Contributions: Royal Ontario Museum, 123*, 1–112.
741
742
743
744
745
746
747
748
749
750
751
752
753
754
755
756
757
758
759
760
761
762

ANEXOS

APPENDIX 1. List of synapomorphies for each clade and terminal táxon.

***Abramites hypselonotus*:**
Char. 15: 1 → 0
Char. 39: 0 → 1
Char. 40: 0 → 1

***Anostomoides atrianalis*:**
Char. 13: 1 → 0
Char. 26: 0 → 1
Char. 32: 3 → 2
Char. 100: 1 → 0

***New genus*:**
Char. 11: 0 → 1
Char. 20: 0 → 1
Char. 35: 0 → 1
Char. 39: 0 → 1
Char. 41: 1 → 0
Char. 43: 1 → 2
Char. 66: 0 → 1
Char. 69: 0 → 1
Char. 94: 2 → 1

***Anostomus anostomus*:**
Char. 13: 1 → 0

***Anostomus ternetzi*:**
Char. 100: 1 → 0

***Leporinus scalabrinii*:**
No autapomorphies

***Gnathodolus bidens*:**
Char. 3: 0 → 1
Char. 10: 1 → 0
Char. 20: 0 → 1
Char. 23: 1 → 0
Char. 32: 3 → 2
Char. 39: 0 → 1
Char. 41: 1 → 2
Char. 57: 0 → 1
Char. 70: 0 → 1
Char. 73: 1 → 0
Char. 77: 2 → 0

***Hypomasticus despaxi*:**
Char. 12: 0 → 1
Char. 32: 1 → 2
Char. 36: 4 → 3
Char. 37: 0 → 2
Char. 118: 1 → 0
Char. 120: 0 → 1
Char. 121: 0 → 1

***Hypomasticus megalepis*:**
Char. 19: 1 → 0
Char. 119: 0 → 1

***Hypomasticus mormyrops*:**
Char. 12: 0 → 1

***Hypomasticus pachycheilus*:**
Char. 5: 1 → 2
Char. 8: 2 → 1
Char. 119: 0 → 1

***Laemolyta garmani*:**
No autapomorphies

***Laemolyta orinocensis*:**
No autapomorphies

***Laemolyta proxima*:**
Char. 18: 1 → 0
Char. 105: 1 → 0

***Laemolyta taeniata*:**
No autapomorphies

***Leporellus pictus*:**
No autapomorphies

***Leporellus vittatus*:**
Char. 33: 1 → 3

***Leporinus agassizi*:**
Char. 27: 1 → 0
Char. 32: 3 → 2
Char. 33: 3 → 2
Char. 118: 1 → 0

***Leporinus aripuanensis*:**
Char. 9: 0 → 1
Char. 32: 3 → 1
Char. 33: 3 → 2

***Leporinus* cf. *ecuadorensis*:**
Char. 5: 1 → 2
Char. 32: 3 → 2
Char. 33: 3 → 2
Char. 63: 0 → 1

***Leporinus* cf. *fasciatus*:**
No autapomorphies

***Leporinus* cf. *moralesi*:**
Char. 27: 1 → 0
Char. 31: 4 → 3
Char. 40: 0 → 1
Char. 42: 1 → 2
Char. 105: 1 → 0

***Leporinus* cf. *niceforoi*:**
Char. 72: 1 → 0
Char. 92: 1 → 0

***Leporinus fasciatus*:**
No autapomorphies

***Leporinus friderici*:**

No autapomorphies

***Leporinus gomesi*:**

Char. 119: 0 → 1

Char. 122: 0 → 2

***Leporinus jatuncochi*:**

Char. 15: 1 → 0

Char. 35: 0 → 2

Char. 36: 4 → 3

Char. 37: 0 → 1

***Leporinus ortomaculatus*:**

Char. 9: 0 → 1

Char. 119: 0 → 1

***Leporinus pellegrini*:**

Char. 9: 0 → 1

Char. 105: 1 → 0

***Leporinus striatus*:**

Char. 105: 1 → 0

Char. 120: 0 → 1

Char. 121: 0 → 1

***Leporinus tigrinus*:**

Char. 8: 2 → 3

Char. 9: 0 → 1

Char. 105: 1 → 0

***Petulanos intermedius*:**

No autapomorphies

***Petulanos plicatus*:**

Char. 97: 0 → 1

***Pseudanos gracilis*:**

Char. 5: 2 → 1

***Pseudanos irinae*:**

No autapomorphies

***Pseudanos trimaculatus*:**

No autapomorphies

***Pseudanos winterbottomi*:**

No autapomorphies

***Rhytiodus argenteofuscus*:**

Char. 8: 2 → 1

***Rhytiodus lauzannei*:**

No autapomorphies

***Rhytiodus microlepis*:**

No autapomorphies

***Sartor elongatus*:**

Char. 82: 0 → 1

Char. 99: 1 → 0

Char. 106: 1 → 0

***Schizodon fasciatus*:**

No autapomorphies

***Schizodon isognathus*:**

Char. 3: 0 → 1

Char. 7: 0 → 1

Char. 27: 1 → 0

***Schizodon knerii*:**

Char. 3: 0 → 1

Char. 7: 0 → 1

Char. 27: 1 → 0

Char. 59: 0 → 1

***Schizodon nasutus*:**

Char. 5: 1 → 2

Char. 8: 2 → 1

Char. 15: 1 → 0

Char. 46: 1 → 0

Char. 56: 0 → 1

Char. 92: 0 → 1

***Schizodon scotorhabdotus*:**

Char. 95: 3 → 2

Char. 112: 1 → 0

***Schizodon vittatus*:**

Char. 80: 1 → 0

***Synaptolaemus cingulatus*:**

Char. 24: 0 → 1

Char. 42: 1 → 3

Char. 92: 1 → 0

Char. 116: 0 → 1

***Brycon falcatus*:**

Char. 5: 1 → 2

Char. 8: 1 → 0

Char. 32: 5 → 3

Char. 33: 5 → 3

Char. 37: 4 → 5

Char. 87: 0 → 1

***Caenotropus maculosus*:**

Char. 36: 4 → 12

Char. 112: 1 → 0

***Caenotropus mestomorgmatos*:**

No autapomorphies

***Chilodus punctatus*:**

Char. 86: 0 → 1

Char. 112: 1 → 2

***Citharinus* sp.:**

Char. 13: 0 → 1

Char. 92: 1 → 0

Char. 94: 2 → 0

Char. 96: 2 → 0

Char. 129: 0 → 1

Char. 135: 0 → 1

Char. 139: 0 → 1

Char. 151: 0 → 1

***Curimata inornata*:**

No autapomorphies

***Curimatopsis microlepis*:**

Char. 8: 1 → 0

Char. 12: 0 → 1

Char. 87: 0 → 1

Char. 94: 0 → 1

Char. 96: 0 → 1

***Distichodus* sp.:**

No autapomorphies

Hemiodus ocellatus:

Char. 22: 1 → 2

Char. 36: 7 → 0

Char. 125: 0 → 1

Char. 131: 0 → 1

Char. 153: 0 → 1

***Parodon suborbitalis*:**

Char. 12: 0 → 1

Char. 22: 1 → 2

Char. 28: 0 → 1

Char. 31: 5 → 4

Char. 36: 7 → 3

Char. 37: 4 → 6

Char. 45: 0 → 1

Char. 49: 0 → 1

Char. 90: 1 → 0

Char. 91: 0 → 1

Char. 92: 1 → 0

Char. 125: 0 → 1

Char. 130: 0 → 1

***Potamorhina laticeps*:**

Char. 2: 0 → 1

Char. 12: 0 → 2

Char. 112: 1 → 2

Char. 115: 0 → 1

Prochilodus rubrotaeniatus:

Char. 5: 1 → 2

Char. 12: 0 → 2

Char. 105: 0 → 1

***Semaprochilodus insignis*:**

Char. 2: 0 → 1

Char. 8: 1 → 3

Char. 123: 0 → 1

***Xenocharax spilurus*:**

Char. 76: 1 → 0

Char. 90: 1 → 0

Node 63:

Char. 28: 0 → 1

Node 64:

Char. 5: 1 → 2

Char. 8: 2 → 1

Char. 25: 0 → 1

Char. 31: 4 → 3

Char. 32: 3 → 2

Char. 33: 3 → 2

Char. 34: 1 → 0

Char. 106: 1 → 0

Char. 118: 1 → 0

Node 65:

Char. 27: 0 → 1

Char. 32: 1 → 3

Char. 33: 2 → 3

Char. 94: 2 → 1

Node 66:

Char. 2: 0 → 1

Char. 15: 0 → 1

Char. 19: 1 → 0

Char. 34: 0 → 1

Node 67:

Char. 1: 0 → 1

Char. 13: 0 → 1

Char. 33: 1 → 2

Char. 67: 0 → 1

Char. 68: 0 → 1

Node 68:

Char. 18: 0 → 1

Char. 49: 0 → 1

Char. 52: 1 → 0

Char. 76: 0 → 1

Char. 87: 0 → 1

Char. 96: 2 → 1

Char. 118: 0 → 1

Node 69:

Char. 22: 1 → 0

Char. 31: 5 → 4

Char. 37: 4 → 0

Char. 38: 1 → 0

Char. 45: 0 → 1

Char. 50: 1 → 0

Char. 51: 1 → 0

Char. 62: 0 → 1

Char. 65: 1 → 0

Char. 73: 0 → 1

Char. 83: 0 → 1

Char. 84: 0 → 1

Char. 85: 2 → 0

Char. 90: 1 → 0

Char. 91: 0 → 1

Char. 106: 0 → 1

Char. 107: 0 → 1

Char. 134: 0 → 1

Node 70:

Char. 23: 0 → 1
Char. 36: 7 → 4
Char. 46: 0 → 1
Char. 71: 2 → 0
Char. 136: 0 → 1
Char. 137: 0 → 1
Char. 139: 0 → 1
Char. 142: 0 → 1
Char. 144: 0 → 1
Char. 148: 0 → 1
Char. 150: 0 → 1
Char. 152: 0 → 1
Char. 157: 0 → 1

Node 71:

Char. 32: 5 → 1
Char. 33: 5 → 1
Char. 52: 0 → 1
Char. 129: 0 → 1
Char. 149: 0 → 1
Char. 151: 0 → 1

Node 72:

Char. 2: 1 → 0
Char. 106: 1 → 0

Node 73:

Char. 76: 1 → 0
Char. 111: 1 → 0
Char. 115: 1 → 0
Char. 158: 1 → 0

Node 74:

Char. 32: 2 → 5
Char. 33: 2 → 5
Char. 52: 1 → 0
Char. 108: 2 → 0
Char. 130: 1 → 0
Char. 155: 1 → 0
Char. 156: 1 → 0

Node 75:

Char. 2: 0 → 1
Char. 87: 1 → 0
Char. 140: 1 → 0

Node 76:

No synapomorphies

Node 77:

Char. 65: 0 → 1
Char. 90: 0 → 1
Char. 92: 1 → 0
Char. 106: 1 → 0
Char. 120: 0 → 1

Node 78:

Char. 80: 0 → 1
Char. 117: 0 → 1

Node 79:

Char. 28: 0 → 1
Char. 121: 0 → 1

Node 80:

Char. 2: 1 → 0
Char. 19: 0 → 1
Char. 22: 0 → 2
Char. 71: 0 → 1
Char. 89: 1 → 0
Char. 90: 1 → 0
Char. 92: 0 → 1

Node 81:

Char. 4: 0 → 1
Char. 12: 0 → 1
Char. 14: 0 → 1
Char. 17: 1 → 0
Char. 21: 0 → 1
Char. 27: 1 → 0
Char. 50: 0 → 1
Char. 67: 1 → 0
Char. 72: 1 → 2
Char. 81: 0 → 1
Char. 85: 0 → 1
Char. 105: 1 → 0
Char. 106: 0 → 1

Node 82:

Char. 8: 2 → 1
Char. 38: 0 → 1
Char. 46: 1 → 2
Char. 117: 1 → 0

Node 83:

Char. 41: 1 → 2
Char. 42: 1 → 2
Char. 58: 0 → 1

Node 84:

Char. 35: 0 → 1
Char. 37: 0 → 1
Char. 54: 0 → 1
Char. 61: 1 → 0

Node 85:

Char. 14: 1 → 0
Char. 43: 3 → 1
Char. 51: 0 → 1
Char. 66: 0 → 1
Char. 86: 0 → 1

Node 86:

Char. 41: 2 → 1

Char. 42: 2 → 1

Char. 52: 0 → 1

Char. 78: 0 → 1

Char. 99: 0 → 1

Char. 120: 1 → 0

Node 87:

Char. 9: 0 → 1

Char. 31: 4 → 3

Node 88:

Char. 16: 0 → 1

Char. 22: 0 → 1

Char. 46: 1 → 0

Char. 55: 0 → 1

Char. 56: 0 → 1

Node 89:

Char. 40: 0 → 1

Char. 47: 0 → 1

Char. 96: 1 → 2

Node 90:

Char. 11: 0 → 1

Char. 41: 2 → 0

Char. 42: 2 → 0

Char. 92: 0 → 1

Node 91:

Char. 117: 0 → 1

Node 92:

Char. 32: 3 → 4

Char. 33: 3 → 4

Node 93:

Char. 17: 1 → 0

Char. 26: 0 → 1

Char. 32: 1 → 2

Char. 64: 0 → 1

Char. 93: 0 → 1

Char. 98: 0 → 1

Char. 114: 0 → 1

Char. 123: 0 → 1

Node 94:

Char. 111: 0 → 1

Char. 116: 0 → 1

Char. 118: 1 → 0

Node 95:

Char. 31: 4 → 3

Node 96:

Char. 5: 2 → 1

Char. 8: 1 → 2

Char. 32: 3 → 2

Char. 88: 0 → 1

Node 97:

Char. 100: 1 → 0

Char. 118: 0 → 1

Char. 120: 1 → 0

Node 98:

Char. 6: 0 → 1

Char. 11: 0 → 1

Char. 29: 0 → 1

Char. 101: 0 → 1

Char. 102: 0 → 1

Char. 104: 0 → 1

Node 99:

Char. 7: 1 → 0

Char. 30: 0 → 1

Char. 40: 0 → 1

Char. 44: 0 → 1

Char. 63: 0 → 1

Char. 94: 1 → 2

Char. 113: 0 → 1

Node 100:

Char. 103: 0 → 1

Char. 115: 0 → 1

Char. 120: 1 → 0

Node 101:

Char. 69: 0 → 1

Char. 120: 1 → 0

Node 102:

Char. 33: 3 → 4

Char. 41: 2 → 3

Char. 42: 2 → 3

Char. 55: 0 → 1

Char. 109: 0 → 1

Node 103:

Char. 17: 1 → 2

Char. 41: 3 → 2

Char. 42: 3 → 2

Char. 59: 0 → 1

Char. 72: 1 → 0

Char. 117: 1 → 0

Node 104:

Char. 16: 0 → 1

Char. 101: 0 → 1

Char. 102: 0 → 1

Node 105:

Char. 11: 0 → 1

Char. 77: 0 → 1

Char. 94: 2 → 1

Char. 128: 0 → 1

Char. 131: 0 → 1

Node 106:

Char. 5: 1 → 0

Char. 31: 5 → 0

Char. 36: 7 → 0

Char. 76: 0 → 1

Char. 92: 1 → 0

Char. 125: 0 → 1

Char. 131: 0 → 1

Node 107:

Char. 94: 2 → 0

Char. 96: 2 → 0

Char. 126: 0 → 1

Char. 127: 0 → 1

Char. 135: 0 → 1

Char. 138: 0 → 1

Char. 140: 0 → 1

Char. 141: 0 → 1

Char. 143: 0 → 1

Char. 145: 0 → 1

Char. 146: 0 → 1

Char. 147: 0 → 1

Char. 153: 0 → 1

Char. 154: 0 → 1

Node 108:

Char. 22: 1 → 2

Char. 51: 1 → 0

Char. 62: 0 → 1

Char. 65: 1 → 0

Char. 83: 0 → 1

Char. 84: 0 → 1

Char. 85: 2 → 0

Char. 128: 0 → 1

Char. 134: 0 → 1